UNIVERSIDADE DE LISBOA
FACULDADE DE CIÊNCIAS

Faculdade de Ciências

Departamento de Biologia

Diet and trophic relationships of top predators in the oceanic region of the archipelago of Madeira

"Documento Definitivo"

Doutoramento em Biologia e Ecologia das Alterações Globais

Especialidade em Biologia e Ecologia Marinha

Joana Chalbert Manso Romero

Tese orientada por:

José Pedro Granadeiro
Paulo Catry

Documento especialmente elaborado para a obtenção do grau de doutor

2020

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Documento especialmente elaborado para a obtenção do grau de doutor

Fundação para a Ciência e a Tecnologia (FCT) – Bolsa de Doutoramento (PD/BD/127810/2016)
Fundação para a Ciência e a Tecnologia (FCT) – Projecto Oceanwebs (PTDC/MAR-PRO/0929/2014)
Fundação para a Ciência e a Tecnologia (FCT) – Projecto Seamigrant (PTDC/BIA-ANM/3743/2014)
Fundação para a Ciência e a Tecnologia (FCT) – Financiamento estratégico atribuído ao CESAM (UIDB/50017/2020, UIDP/50017/2020)
Fundação para a Ciência e a Tecnologia (FCT) – Financiamento estratégico atribuído ao MARE (UIDB/04292/2020, UIDP/04292/2020)
Comissão Europeia – Projecto LIFE RECOVER NATURA (LIFE12 NAT/PT/000195)
Agência Regional para o Desenvolvimento da Investigação, Tecnologia e Inovação (ARDITI) – Projecto (M1420-01-0145-FEDER-000001-Observatório Oceânico da Madeira-OOM)

2020

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Lisboa, dezembro de 2020
Joana C. M. Romero

Para os meus pais,
Por sempre me apoiarem e acreditarem em mim.

"O rapaz, porém, pensava no seu tesouro. Quanto mais perto ficava do seu sonho, mais difíceis se tornavam as coisas. Já não funcionava aquilo que o velho rei tinha chamado "sorte de principiante". O que funcionava, sabia ele, era o teste da persistência e da coragem de quem procura a sua Lenda Pessoal. Por isso ele não podia apressar-se, nem ficar impaciente. Se agisse assim, ia acabar por não ver os sinais que Deus tinha posto no seu caminho"

O Alquimista, Paulo Coelho

Agradecimentos/ Acknowledgements

Em primeiro lugar, gostaria de agradecer aos meus orientadores, José Pedro Granadeiro e Paulo Catry, por todo o apoio e ajuda prestados durante estes quatro anos de doutoramento. Agradeço a confiança que depositaram em mim e todo o tempo que disponibilizaram para me ensinar e guiar. Estes quatro anos convosco foram uma constante aprendizagem, tanto no campo e laboratório, como a nível académico. Só posso esperar ter conseguido absorver todo o conhecimento e ensinamentos que tinham para me dar. Também vos quero agradecer pelos momentos de amizade e pelos "dar na cabeça" que tão importantes foram para o meu crescimento enquanto investigadora e pessoa. Por isto tudo, um muito obrigada!

Também gostaria de agradecer a todas as entidades que estiveram envolvidas nos trabalhos desta tese ou que de alguma forma possibilitaram a realização da mesma. À Fundação para a Ciência e Tecnologia e ao Centro de Estudos do Ambiente e do Mar, pela atribuição da bolsa que me permitiu ingressar nesta aventura. À Faculdade de Ciências da Universidade de Lisboa por me albergar. Ao Instituto das Florestas e Conservação da Natureza, nomeadamente ao Doutor Paulo Oliveira, Dra. Dília Menezes, Dra. Carolina Santos, Dra. Nádia Coelho e Dr. Pedro Sepulveda, pela ajuda financeira e logística prestada nos diferentes trabalhos realizados nas Desertas e Selvagens. À Direcção Regional das Pescas da Madeira, nomeadamente ao Dr. João Delgado e Dra. Graça Faria, pela disponibilização das instalações e apoio logístico e financeiro providenciados ao projecto. Gostaria também de agradecer a ajuda e apoio indispensáveis da Doutora Margarida Hermida e das bolseiras Bárbara Cavaleiro e Raquel Segur, na recolha de amostras e dados de atuns e ruama na Madeira.

Todo o trabalho que realizei ao longo destes quatro anos não teria tido o mesmo sabor sem a presença, companheirismo e amizade do pessoal da FCUL. Filipe Moniz, muito obrigada pela ajuda dada na Selvagem e no laboratório, pelo passar de conhecimento sobre técnicas de captura de gaivotas e manuseamento de cagarras, "Bebe chico!", mas acima de tudo pela amizade. À minha PhD-sister, Marie Claire Gatt, muito obrigada pelos momentos memoráveis na Selvagem e nas viagens de navio entre a Madeira e Selvagem (talvez nos queiramos esquecer desta parte), pelas conversas e trocas de ideias sobre as nossas teses, pela ajuda com o R sempre que ele não colaborava comigo. Também gostava de agradecer à Letizia Campioni, a minha companhia na sala. Muito obrigada pelos conselhos e "brainstormings" e, acima de tudo, pela ajuda e companhia na

Selvagem. Ao meu companheiro de laboratório, Fernando Madeira. Antes de tudo quero pedir-te desculpa pelos maus cheiros que tiveste de suportar, cenas de atuns! Muito obrigada pelas horas infindáveis de conversa e parvoíce, sem dúvida foram a melhor companhia que podia ter tido para suportar os longos dias e meses a identificar vértebras e coisas afins. Um grande obrigada à Carolina Vieira pela sua dedicação e ajuda na identificação de fito- e zooplâncton, pela sua vontade de aprender e fazer melhor. Também gostaria de agradecer a todos os outros membros do Wings over water, ao Francesco Ventura, Ana Cordeiro, Edna Correia, Jorge Gutiérrez, Patrícia Pedro, Mohamed Henriques, Maria Alho, Carolina Vieira, João Belo, João Paulino, Martin Beal, Anne-Sophie, Mónica Silva, Vera Nunes, Rita Patrício, Ricardo Furtado, Amadú Insambé, Tumbulo Garcia, Daniel Lopes, Teresa Catry e Rui Rebelo, pelas trocas de ideias, dicas e conhecimento trocados ao longo destes anos.

Não poderia deixar de agradecer à Maria Alho por estar sempre presente em todo este processo, às vezes, um pouco doloroso. Obrigada pelas conversas sobre tudo e sobre nada, à partilha das alegrias e das coisas menos boas, por aturares os meus desesperos e inseguranças. Por estares sempre lá para ouvir-me e por seres a pessoa fantástica que és. Sem dúvida, ajudaste-me a aligeirar as "dores" do doutoramento.

A todos os que me ajudaram no campo e laboratório ao longo destes anos, muito obrigada. Ao João Morgado, Estefania, Paulo Catry, Marie Claire, Maria Alho, Fernando Madeira, Filipe Moniz, Letizia Campioni, Diana Barão, José Pedro Granadeiro, Teresa Catry, Carolina Vieira, Mafalda Pádua, Gabriel Mendes, Rafael Luís e Washington Gouveia. Um grande obrigada também a todos os vigilantes da natureza que ajudaram em toda a logística relacionada com as estadias na Selvagem e Desertas: Jacques da Mata, Fernando Vieira, Carlos Clemente, Carlos Santos, Manuel José, Isamberto Silva, João Paulo Mendes, Maurício Baptista e Marco Camacho.

Um agradecimento muito especial à Dona Augusta e Pierre por todo o carinho e atenção. Por me receberem sempre tão bem na Guiné mas, especialmente, nesta última visita, por me terem proporcionado o melhor ambiente que poderia ter para "atacar" os últimos capítulos da tese. Obrigada por me mostrarem sítios maravilhosos, pelas ostradas de sábado e todas as iguarias preparadas pela Dona Augusta. Um obrigada muito grande também para a Fanceni, Lu e Lara. A vossa companhia foi sempre uma lufada de ar fresco para começar mais uma semana de trabalho. Pelos domingos preguiçosos no terraço e conversas sobre a vida e o mundo, aos nossos jogos da Disney e, sobretudo, ao "Mateus". Que venham muitos mais momentos como estes.

À minha família, por todo o apoio, amor e carinho que sempre me deram. Por acreditarem em mim e darem-me a força que preciso para continuar. Vocês são e serão sempre a minha "casa" e para onde eu vou querer sempre voltar. Um especial obrigada ao meu irmão por me espicaçar a ser melhor, por me incentivar a sair da minha zona de conforto. Obrigada por estares sempre lá para mim. Obrigada ao meu sobrinho do coração, Du (sim, para mim serás sempre Du, por muito que cresças), por seres o único que realmente me conseguia tirar a cabeça do trabalho e problemas com a tua energia, vivacidade e alegria. Nunca deixes de ser o meu "louquinho". Aos meus pais… Não tenho palavras para vos descrever o quão agradecida estou por tudo o que fizeram por mim. A pessoa que sou hoje deve-se aos vossos esforços, dedicação e amor incondicional e, por isso, devo-vos tudo. Obrigada por terem acreditado e puxado por mim e, acima de tudo, por me terem proporcionado a vida e experiências que tive até hoje.

Por fim, mas não menos importante, ao Mo. Obrigada pela pessoa que és e que tens sido para mim, pela tua amizade e amor. Obrigada por me teres "aturado" nestes quatro anos de ausências, muito trabalho e stress, mas também de alegria e novas conquistas. Obrigada pela tua compreensão e paciência mesmo nos dias mais difíceis, pela força e apoio que me deste e por me ajudares a levantar mesmo quando eu já não tinha forças. Obrigada por estares lá todos os dias mesmo quando a distância era grande. Obrigada pelos "brainstormings", comentários aos manuscritos e por tomares conta de mim ao longo de todo este percurso. Obrigada ao meu companheiro, colega e "role-model", não teria sido capaz sem ti a meu lado. Mais do que ontem e menos do que amanhã.

Contents

Resumo

Os estudos de dieta são um elemento importante na compreensão da ecologia de uma espécie, mas são muitas vezes negligenciados e a sua importância subestimada. A dieta de um organismo permite conhecer o habitat em que o animal vive e as suas adaptações ao meio ambiente, mas também permite saber sobre interações com outras espécies. É a combinação de estudos de dieta de várias espécies que permite construir cadeias alimentares e compreender a estrutura e o funcionamento dos ecossistemas. A aplicação deste tipo de estudos no meio marinho tem importância acrescida, uma vez que estudos baseados em observação directa não são suficientes. Esta importância é ainda mais acentuada nas regiões oceânicas, onde as densidades de organismos são baixas e o seu estudo é um desafio.

Esta tese tem como objetivo estudar a dieta e as relações tróficas entre os predadores de topo e as suas presas na região oceânica do arquipélago da Madeira. A dieta e as áreas de alimentação de espécies de importância ecológica e económica, como atuns, aves marinhas e pequenos peixes pelágicos, foram estudadas na tentativa de compreender a sua posição e o seu papel na cadeia alimentar deste ambiente oceânico.

A dieta de duas espécies de peixes pelágicos, a cavala *Scomber colias* e o carapau-negrão *Trachurus picturatus*, foi analisada com base na identificação do conteúdo estomacal de indivíduos capturados ao longo de um ano, nas proximidades da ilha da Madeira. Ambas as espécies são planctívoras e piscívoras, alimentando-se sobretudo de copépodes calanóides e ciclopóides, e de pequenos agulhões *Scomberesox saurus*, clupeídeos, apara-lápis *Macroramphosus scolopax* e mictofídeos.

A dieta do patudo *Thunnus obesus* e do gaiado *Katsuwonus pelamis*, foi estudada identificando o conteúdo estomacal de indivíduos apanhados na Madeira e confirmada através da análise de mercúrio nos tecidos dos atuns e de outros dois peixes epipelágicos, a bicuda *Sphyraena viridensis* e o charuteiro Seriola rivoliana. A dieta de ambas as espécies de atum é composta principalmente por espécies epipelágicas, como a cavala e o peixe-rei *Atherina* sp., o que contrasta com o comportamento e dieta mesopelágicos do patudo em outras regiões do mundo.

Também investigámos a utilização de recursos marinhos pela gaivota-de-patas-amarelas *Larus michahellis atlantis* no arquipélago da Madeira. Esta ave costeira mostrou uma grande dependência antropogénica, com elevado uso de ambientes terrestres e associados ao homem. As poucas vezes que utilizou o meio marinho foi, principalmente,

à noite e em associação com embarcações de cerco. A sua dieta refletiu este comportamento, sendo maioritariamente composta por resíduos e alguns peixes.

O estudo da variação na composição de espécies epipelágicas na vasta região da corrente das Canárias, foi realizado utilizando as aves marinhas como indicadores. Com recurso a viagens de alimentação e regurgitos de cagarras *Calonectris borealis* a nidificar nas Ilhas Selvagens, recolhidos por um período de sete anos, este estudo conseguiu detetar uma alteração na comunidade de peixes pelágicos, com um aumento acentuado da população de apara-lápis nos arredores das ilhas Selvagens, em 2017/2018.

Por fim, desenvolvemos um modelo baseado no equilíbrio de biomassas de espécies encontradas na Zona Económica Exclusiva do arquipélago da Madeira, utilizando o software Ecopath with Ecosim. Este capítulo reuniu as informações recolhidas nos outros capítulos e juntou-as aos dados disponíveis na literatura. O nosso modelo estimou uma elevada biomassa de produtores primários, zooplâncton, outros crustáceos e invertebrados, mas também de pequenos peixes pelágicos e mesopelágicos, que foram considerados o principal alimento de predadores de topo. O ecossistema caracterizou-se por um baixo número de ligações entre os níveis tróficos, que está relacionado com uma dieta mais especializada por parte de organismos como golfinhos, aves marinhas e grandes peixes pelágicos. Apesar de o ecossistema ter apresentado um nível trófico médio baixo, o nível trófico das pescas foi bastante alto por, na Madeira, predadores de topo como atuns e peixe-espada, serem os mais pescados. Os predadores de topo também foram considerados importantes modeladores do ecossistema, sendo designados por espécies-chave.

Palavras-chave: Dieta, Áreas de alimentação, Relações tróficas, Predadores de topo, Cadeia alimentar.

Abstract

Diet studies are important for the understanding of the ecology of species, but commonly overlooked and their importance underestimated. The diet of an organism reveals its prey composition, but also its habitat and foraging behaviour. It also allows to have an insight on the interactions with other species and its surroundings. The combined information of diet studies of several species allows to build food webs and understand the structure and functioning of ecosystems. The application of these studies in the marine environment is particularly important, as pure observational studies are not enough. Such importance is even greater in oceanic regions where densities of organisms are low, and their study is challenging.

This thesis aims to study the diet and trophic relationships of top predators and their prey in the oceanic region of the archipelago of Madeira. The diet and foraging areas of ecologically and economically important species, like tunas, seabirds and small pelagic fish, were studied in the attempt to understand their position and role in the food web of this oceanic environment.

The diet of two species of mackerels, the Atlantic chub mackerel *Scomber colias* and the Blue jack mackerel *Trachurus picturatus*, was assessed using stomach contents of individuals caught throughout a year in the vicinities of Madeira island. These are planktivorous and piscivorous species, feeding mostly on calanoid and cyclopoid copepods, and on very small Atlantic saury *Scomberesox saurus*, clupeids, Longspine snipefish *Macroramphosus scolopax*, and myctophids.

The diet of the Bigeye tuna *Thunnus obesus* and Skipjack tuna *Katsuwonus pelamis*, was assessed using stomach contents and confirmed using mercury analysis in the tissues of tunas and two other epipelagic fish, the Yellowmouth barracuda *Sphyraena viridensis* and the Longfin yellowtail *Seriola rivoliana*. The diet of both species was mainly composed by epipelagic prey, like Atlantic chub mackerel and Sand smelts *Atherina* sp., which contrasts with the mesopelagic behaviour and diet of Bigeye tunas elsewhere.

We also investigated the use of marine resources by the Yellow-legged gull *Larus michahellis atlantis* in the archipelago of Madeira. This coastal bird showed a great anthropogenic dependence, with high use of terrestrial and human-associated environments. The few times it used the marine environment, it was mostly at night and

in association with purse-seine vessels. Its diet reflected this behaviour, being mainly composed by human residues and few fish.

The variation in the composition of epipelagic species through a period of seven years in the broad Canary current region was studied using foraging trips and regurgitations of Cory's shearwaters *Calonectris borealis* nesting on Selvagens Islands. This study was able to depict a shift in the community, with a steep increase of the population of Longspine snipefish in the surroundings of Selvagens islands in 2017/2018.

Finally, we developed a mass-balanced model of the Exclusive Economic Zone of the archipelago of Madeira, using the software Ecopath with Ecosim. This chapter brought together the information collected in the other chapters with data available in the literature. The Madeira system was characterized by high biomass of primary producers, zooplankton and other crustaceans and invertebrates, together with small epipelagic and mesopelagic fish, which were also the main prey of top predators. The food web was characterized by a more linear-like food chain, in opposition to a more web-like food chain, with a large proportion of more specialized organisms, like dolphins, shearwaters and large pelagic fish. Despite the low mean trophic level of the system, the mean trophic level of fisheries was very high, targeting mainly top predators, like tunas and Black scabbardfish, which were also the components with most impact in the ecosystem.

Keywords: Diet, Foraging areas, Trophic relationships, Top predators, Food web.

CHAPTER 1

Credits: Joana Romero

General Introduction

The study of oceanic environments has always represented a challenge for researchers due to the difficulties in sampling this ecosystem, but this is changing with the development of technology and increasing investment in the exploration of the ocean. Many advancements have been made in the understanding of the functioning of oceans, in terms of physical, chemical, and biological processes, but there is still a lot we do not understand. For one, there are still many questions on the impacts of global changes, pollution, and fisheries on the biodiversity and balance of marine ecosystems. One way to address these questions is by assessing the diet of predators, which are wide ocean wanderers, and their trophic relationships with the remaining species of the oceanic food web.

Diet and Foraging Ecology in Marine Ecosystems

Diet studies are essential for the understanding of organisms and their adaptation to the environment. In addition of allowing to study the timing and frequency of feeding (e.g. Granadeiro et al. 1998), energy budgets (e.g. Doidge & Croxall 1985) and competition and interaction among species (e.g. Spitz et al. 2006), diet studies also provide information on prey communities, such as composition, distribution, age and reproduction (e.g. Di Beneditto & Siciliano 2007). Moreover, it can provide insights on the interactions of different species with the fisheries industry (e.g. Wallace et al. 2009), and on the impacts of global changes and human activities on marine species (e.g. Miller & Sydeman 2004).

There are several ways to study the diet of a species, one being the use of stomach contents. For most species the collection of stomach contents requires the animal to be dead, as it is the case of fish and cetaceans, but for others, like seabirds, it is possible to sample their contents in spontaneous regurgitations, or by stomach-flushing (Barrett et al. 2007). Diet analysis is also possible by simply collecting pellets (an agglomerate of hard structures) that are naturally regurgitated after feeding events. The use of stomach contents is usually the most complete method and with higher resolution to describe the diet composition of a species (Karnovsky et al. 2012), as it is often possible to count the number of ingested prey and to identify each organism using morphological characteristics. Even if more digested, prey can still be identified using hard parts, like bones, otoliths, cephalopod beaks, shells, etc. (Granadeiro & Silva 2000, Xavier & Cherel 2009). In more recent years, the development of polymerase chain reaction-based

techniques (PCR) and DNA barcoding have become a powerful ally of this method, making possible the identification of the prey consumed using only a small portion of tissue (Alonso et al. 2014, Correia et al. 2019). Metabarcoding analysis has also proved most useful in studies using faeces, for instance, as it allows to depict more than one prey taxa/species (Ford et al. 2016, Correia et al. 2019). The use of these techniques to identify prey is not always possible due to the high monetary costs they entail and the complexity of the methods. The size and weights of prey are also possible to take in most cases, either through direct observation or using pre-existing equations relating these variables with the size of hard structures (such as otoliths, vertebrae, beaks) of each prey. Still, the analysis of stomach contents present some drawbacks, like the underestimation of easily digested items and short-temporal representation of the diet, as contents only represent the last meal of the individual (Barrett et al. 2007). Another drawback is that it will only represent the prey of the last feeding event. Thus, a good sample size is required to describe the diet more faithfully.

As an attempt to avoid bias and obtain a more detailed and accurate interpretation of the diet, conventional sampling has been allied to the use of biochemical methods, like stable isotope analysis, fatty acid signature, or mercury analysis. Such assays provide tools to assess trophic interactions, diet data over space and time, and can even narrow down the foraging areas of the consumer (Barrett et al. 2007).

Stable isotope analysis has now been widely used as a tool in diet studies (Cherel et al. 2017, Denda et al. 2017, Morera-Pujol et al. 2018). This methodology requires the collection of tissues, like muscle, blood, feathers, among others, to estimate the nitrogen, carbon or sulfur ratios of the consumers. Isotopes accumulate in tissues in predictable ways, allowing to define the trophic level of the consumer using nitrogen, and to identify the feeding habitat (neritic vs. oceanic and epipelagic vs. demersal) of the prey through the carbon isotope ratio (Layman et al. 2012). Also, depending on the tissue used, it is possible to infer different time frames, from a specific period according to its turnover rate, like it happens when using feathers that were grown during a specific period, to months back in time, when using muscle, or to a few weeks or days ago, using different components of the blood of the study species (Layman et al. 2012). Because stable isotopes reflect the food assimilated by studied individuals, it does not carry the bias of different digestibility of prey. However, there is always the need for background information on the potential preys, their isotopic compositions, and foraging areas for a more truthful interpretation of the isotopic signature of the consumer.

Mercury analysis of tissues, per se, cannot infer the diet of individuals, but when associated with stomach contents or stable isotope analysis, they can be a valuable asset to distinguish between prey groups with different mercury concentrations (Di Beneditto et al. 2011). Mercury can be found in the environment in different ways, and once ingested, it has the capacity of magnifying and accumulating in the tissues of its consumers. Its concentration increases from consumer to consumer up to the top predator, which theoretically possess the highest concentrations of mercury of the food chain. Mercury concentrations are not only related to the level of pollution of a habitat, but also with depth. Mercury concentrations can help distinguish between a mesopelagic/bathypelagic and an epipelagic diet, as deep-ocean species have significantly higher concentrations of mercury than epipelagic species due to the higher rate of microbial-mediated methylation of mercury in sub-thermocline low oxygen waters (Choy et al. 2009). In conclusion, mercury is useful to distinguish prey of similar trophic levels and different depths.

Since the advent of very high frequency tracking (VHF), several technologies have been developed, among them those based on the global positioning system (GPS), which has allowed scientists to collect fine-scale location data for far-ranging species. This technology has made possible the study of behaviour, migration, home ranges, human-wildlife conflict and climate change (Hebblewhite & Haydon 2010), but also the definition of foraging areas (Dragon et al. 2012). Moreover, GPS has made possible to track elusive marine species, like seabirds (e.g. Frederiksen et al. 2012), cetaceans (e.g. Sveegaard et al. 2015), sea turtles (e.g. Godley et al. 2008), and even fish (e.g. Horton et al. 2020). Alone, tracking can specify the location or areas used by an organism, but in synchronization with diet studies, it can also define the distribution area of prey (e.g. Alonso et al. 2018) and describe the interannual fluctuations of prey communities (e.g. Hoskins & Arnould 2014), allowing in its turn to delimit important areas, not only for the consumer but also of its prey.

Marine Trophic Webs

A food web is a representation of the flows of energy and matter created by the interaction among organisms (Cohen et al. 1993). It depicts a complex structure that changes through space and time and which influences population dynamics, and the adaptability and evolution of species (Cohen et al. 1993).

The study of food webs has had the main goal of describing the feeding relationships among species in a community. It is a complex subject that started with the study of simple linear food chains and evolved into the study of more reticulated food webs. Food chain is the representation of links between species, starting in the producer and ending at the top predator. There are two types of food chains, grazing and detritus. The first has autotrophs as the origin of energy and nutrients whereas particulate organic matter is the basal energy source in the detritus food chain. The same food web can be constituted by both types of food chains, and depending on the ecosystem, one or the other or even both, can dominate the food web (Odum 1980, Asmus & Asmus 1985, Han et al. 2017). Different types of food webs have been suggested by Robert Paine based on species of a rocky intertidal zone, the connectedness web, the energy flow web, and the functional web (Paine 1980). The connectedness web is based on observation of feeding links, while the energy flow web, as its name suggests, measures the rate at which energy flows through nodes in the web. Lastly, the functional web reflects only the influence of consumers on the consumed species (Paine 1980). Yet, such webs were still too simple or inaccurate to describe the complexity of the natural food webs, which led to the development of present food web models. The connectedness web was brought together with two fundamental species traits, the biomass and abundance of both consumers and sources (Cohen et al. 2003), allowing for the exploration of more complex interactions between trophic structures.

Food webs represent the union points between all the species of an ecosystem. There are variables and processes that might affect a specific group species, but if the food web remains stable, the ecosystem is more likely to remain in equilibrium. Stable food webs are typically characterised by few strong interactions integrated among a group of weak links (McCann et al. 1998, Neutel et al. 2002). Weak links prevent complex food webs with long loops from being unstable (Neutel et al. 2002) or having chaotic dynamics by dampening the potential destabilizing effects of strong consumer-resource interactions (McCann et al. 1998). A higher number of weak links lowers the mean and variance of interaction strengths and increases local stability in communities (Kokkoris et al. 1999). For these reasons, the disappearance of weak links can be damaging for natural communities by decreasing population abundances, ultimately leading to their extinction (McCann et al. 1998). The existence of smaller food chains with fewer trophic levels and a more web-like look, in opposition to long and unstable food chains with a reduced number of interactions between species with higher strengths, has proven to provide more

stability to food webs (Borrelli & Ginzburg 2014). Therefore, it is expectable that generalist-dominated food webs are prone to exhibiting less fluctuations than specialist-dominated food webs, since generalist species create more links with a lower average interaction strength than specialists (McCann et al. 1998). In the same line, a less productive system will house less species and will tend to have fewer links with larger average interaction strengths. More productive systems house higher biodiversity, which has been linked to stability and a higher resistance and resilience of an ecosystem to perturbations (Kondoh 2003, Ives & Carpenter 2007).

There are different perturbations influencing the oceanic environment (Lu et al. 2018, O'Leary et al. 2020), some of natural origin and some triggered by human activities, but most eventually end up being reflected in the ecology and behavior of its species and, consequently, in the functioning of the food web and the ecosystem (Lavoie et al. 2010, Christianen et al. 2017, Michel et al. 2019). Yet, knowledge on the impacts and implications of global changes and other human activities in marine ecosystem are scarce. For that reason, it is important to study the food web as a whole, so we can better understand the ecosystem and implement holistic management and conservation measures, instead of less effective single-species measures.

Food web models can provide an overview of the food web and of the ecosystem. Among the several existing software and packages is the Ecopath with Ecosim (Christensen & Walters 2004), a mass-balanced trophic model that allows to address ecological questions, like the evaluation of the impacts of fishing activities in ecosystems (e.g. Colléter et al. 2015), placement and effects of marine protected areas, and effects of environmental changes (e.g. Heymans et al. 2014). It further allows to study management policy options (Christensen et al. 2008). However, in order to build the model, it is necessary to gather information on the species of the ecosystem, including knowledge on their biomass and production, and diet composition of each of the functional groups/species. Thus, diet studies are important in an ecosystem perspective and not only for knowledge on the ecology of single species.

The oceanic region of the archipelago of Madeira

The archipelago of Madeira is located off Northwest Africa, in the subtropical front where the cold waters from the north and the warm waters from the south meet. It is composed by three groups of oceanic islands, Madeira, Desertas and Porto Santo, which are surrounded by the Canary and the Azores currents. As most oceanic islands, they have

narrow continental shelves, prolonged by vast abyssal plains that can go as deep as ca. 5,000 m. Three hundred kilometers south of Madeira is the archipelago of Selvagem, and part of the Exclusive Economic Zone (EEZ) of Madeira. The Madeira region is relatively poor when compared to the upwelling systems found in African neritic areas (Cropper et al. 2014). Even so, small and localized upwelling phenomena occur near the coast of the island and in between Madeira and Desertas islands. An underwater ridge resulting from the collapsed volcanic crater is probably causing this upwelling and manifestation of cold and highly productive water at the surface (Caldeira et al. 2002). Furthermore, cold core eddies located in the western side of Madeira and Desertas also showed to increase greatly the productivity in this area (Caldeira et al. 2002). Due to these processes, it is possible for the region to harbour a relevant variety of taxa.

The archipelago of Madeira is an important feeding ground for many species during the warmer months (spring to autumn). Many go there to breed, like seabirds, arriving in the beginning of the spring and leaving only when autumn has started. The Cory's shearwater *Calonectris borealis* is the most abundant seabird species breeding in these islands (Granadeiro et al. 2006), although other common species, like the Bulwer's petrel *Bulweria bulwerii* and the Band-rumped storm-petrel *Hydrobates castro*, also breed in Madeira (Meirinho et al. 2014). Underwater, tunas are among the most iconic figures of "summer" in Madeira, as they are considered a delicacy and, therefore, are highly targeted by fisheries (Gouveia et al. 2019). The Bigeye tuna *Thunnus obesus* and the Skipjack tuna *Katsuwonus pelamis* are the most abundant, but the Albacore tuna *Thunnus alalunga* has known to exceed the abundance of Skipjack tuna in some years (Gouveia et al. 2019). The Atlantic bluefin tuna *Thunnus thynnus* and the Yellowfin tuna *Thunnus albacares* can also be found in these waters (Gouveia et al. 2019). Several species of cetaceans, like Fin whales *Balaenoptera physalus*, also visit these waters during their migrations (Freitas et al. 2012). Many others are resident, like the short-finned pilot whale *Globicephala macrorhynchus*, or are sighted all-year-around, like the Sperm whale *Physeter macrocephalus* (Freitas et al. 2012, 2014). Madeira is also known as a good sport-fishing spot, which reflects the abundance of large predatory pelagic fish, like the Atlantic blue marlin *Makaira nigricans*. Going lower in the trophic web, we will find mackerels (Blue jack *Trachurus picturatus* and Atlantic chub mackerels *Scomber colias*) dominating the intermediate trophic levels (Hermida & Delgado 2016). Other small pelagic fishes are present but in lower abundances, like European pilchard *Sardina pilchardus* and Bogue *Boops boops*. Another iconic species of Madeira is the Scabbard

fish *Aphanopus carbo*, the most captured species by the Madeiran fishing fleet (DREM data), and another touristic attraction of the region.

There are presently unmeasured threats that are impacting oceanic ecosystems, such as human exploitation and climate change, and the assessment of their real impact in these ecosystems directly depends on the existence of good quality baseline information on the ecology of species and interactions among food web components. The oceanic ecosystem around the archipelago of Madeira, despite the recognised importance of its biodiversity and services provided to humans, is still largely understudied and several of the most important components of the food web and their interactions are still unknown.

Thesis outline

The general objective of this work was to assess the trophic web of the oceanic region of the archipelago of Madeira. To tackle this, I first described the diet of key element species from this ecosystem, namely of small pelagic fishes, tunas, and seabirds, of which very few information was available. I also characterized the community of the most common and available epipelagic species of this ecosystem and produced a model which could explain the food web system and interactions of this oceanic region.

This thesis comprises a total of seven chapters: a first chapter which introduces the topics discussed in the following chapters: five chapters (Chapter 2-6) corresponding to a series of five articles (one published, one accepted, two submitted and in revision, and one manuscript in progress); and a last chapter where I provide a general discussion about the chapters presented and the main conclusions of the thesis.

Chapter 2 - Diet and trophic position of two mackerel species in the archipelago of Madeira, Portugal

In this chapter we describe for the first time the diet of the Atlantic chub mackerel *Scomber colias* and Blue jack mackerel *Trachurus picturatus* in the oceanic region of the archipelago of Madeira. These are two of the most abundant and important species in this ecosystem, as prey for many top predators that use this area as a migratory corridor and as feeding grounds. Despite several studies performed in neritic areas, oceanic studies are scarce and information on the feeding ecology of these mackerels is limited in these regions.

Chapter 3 - The diet of the Bigeye tuna *Thunnus obesus* and the Skipjack tuna *Katsuwonus pelamis* in the subtropical pelagic region of the northeast Atlantic

In this chapter we describe for the first time the diet of the Bigeye tuna *Thunnus obesus* and Skipjack tuna *Katsuwonus pelamis* in the archipelago of Madeira. This is the first diet study for the Bigeye tuna in the Northeast Atlantic and only the second for the Skipjack tuna, the first being in the Canary Islands.

Chapter 4 - A gull that scarcely ventures on the ocean: Yellow-legged gulls *Larus michahellis atlantis* on the oceanic island of Madeira

In this chapter we describe the distribution and foraging behaviour of the Yellow-legged gull *Larus michahellis atlantis* in the archipelago of Madeira, using GPS-GSM devices and stable isotope analysis.

Chapter 5 - Seabird diet analysis suggests sudden shift in the pelagic communities of the subtropical Northeast Atlantic

In this chapter we studied the variation in the composition of epipelagic species through time in the broad Canary Current region, by analysing foraging trips and regurgitations of Cory's shearwaters *Calonectris borealis* nesting on Selvagem Grande island in 2008-2011 and 2016-2018. Furthermore, we used fisheries, oceanographic data, and the North Atlantic Oscillation as possible explanatory variables for trends in behaviour and diet of Cory's shearwaters.

Chapter 6 – Food web structure of the subtropical oceanic archipelago of Madeira, eastern North Atlantic

In this chapter we aim to develop an ecosystem-based model of the Exclusive Economic Zone of the archipelago of Madeira, using the Ecopath with Ecosim software. As little-known ecosystems, oceanic environments, like the archipelago of Madeira, are still in need of base line information before we can understand the extent of global changes impacts. This chapter is still a work in progress.

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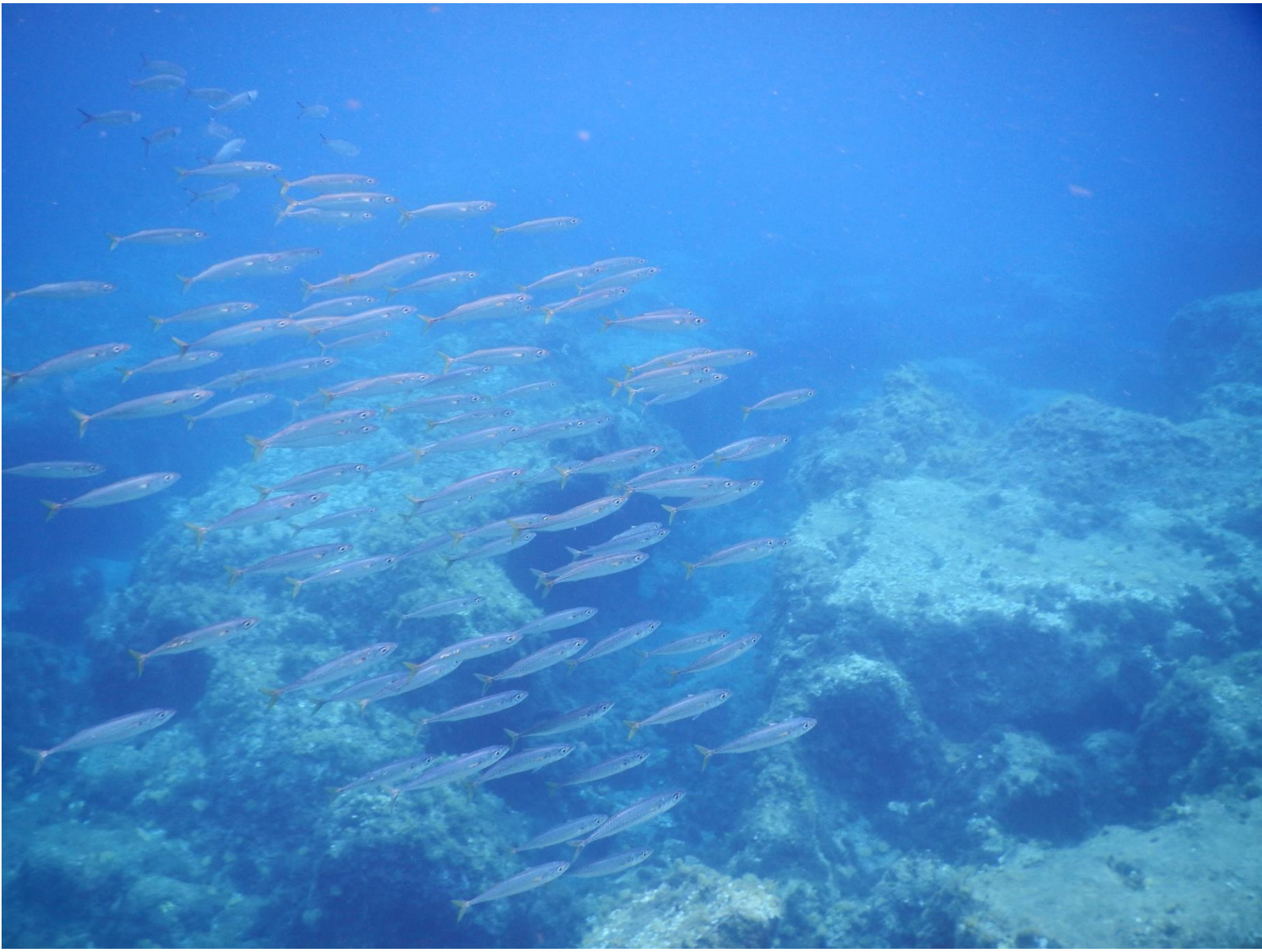
CHAPTER 2



Credits: Joana Romero

This chapter is published as:

Joana Romero, Carolina Vieira*, Susana Garrido, Margarida Hermida, Paulo Catry, Graça Faria, José Pedro Granadeiro (2021). Diet and trophic position of two mackerel species in the archipelago of Madeira, Portugal. Journal of Fish Biology, 202:1-13.*

**contributed equally*

Diet and trophic position of two mackerel species in the archipelago of Madeira, Portugal

Abstract

The Atlantic chub mackerel *Scomber colias* and the Blue jack mackerel *Trachurus picturatus* are two abundant species in the Macaronesia region which include the archipelago of Madeira, Portugal. Both are key species in the trophic web, being important prey for several local top predators, such as seabirds and marine mammals. However, little is known about their feeding ecology in oceanic environments. In this study, we describe the diets of the *S. colias* and the *T. picturatus* in the oceanic region of Madeira throughout a year and by seasons. *Scomber colias* fed on a broader range of prey groups than *T. picturatus*, but for both species, zooplankton (particularly calanoid copepods) and fish were the most important food items, according to stomach contents. The diet of *S. colias* included a higher proportion of fish, namely Atlantic saury *Scomberesox saurus* and *S. colias*, than that of *T. picturatus*, that included mostly Longspine snipefish *Macroramphosus scolopax*. *Trachurus picturatus* also consumed higher proportions of decapods and other copepods. Seasonal variation was found in the diet of both species, with zooplanktonic species being more important in colder months (February to April) for *S. colias* and during warm months (May to October) for *T. picturatus*. Their diet in other seasons were dominated by fish. Despite consuming similar prey, Carbon and Nitrogen stable isotope analysis of muscle of *S. colias* and *T. picturatus* showed little overlap in their diets, and *T. picturatus* showed higher $\delta^{15}N$ and a narrower isotopic niche.

Keywords: Copepods, Diet, Mackerels, Stable isotopes, Stomach contents, Trophic position.

Introduction

The Atlantic chub mackerel *Scomber colias* Gmelin 1789 and the Blue jack mackerel *Trachurus picturatus* Bowdich 1825 are two abundant species in the temperate and subtropical coastal waters of the Atlantic. *Scomber colias* are distributed from the Bay of Biscay to the Azores and down to South Africa (Collette, 1983; Hernández and Ortega, 2000). While *T. picturatus* share the northern limits of *S. colias*, these are restricted to Mauritania in the southern limit (Shaboneyev and Kotlyar, 1979; Shaboneyev and Ryazantseva, 1977). Both *S. colias* and *T. picturatus* occupy the surface layers of the water column but can also go as deep as 300 and 500 m, respectively (Hernández and Ortega, 2000; Menezes *et al.*, 2009). They can also be found in more offshore waters, in seamounts and close to islands, such as those of the archipelago of Madeira, Portugal (Vasconcelos *et al.*, 2012, 2018). These species occupy intermediate trophic levels and are key prey species in the pelagic trophic structure for many predators, such as cephalopods (e.g. Martins, 1982), large pelagic fish, like tunas (e.g. Logan *et al.*, 2011), seabirds (e.g. Alonso *et al.*, 2014; Romero *et al.* 2019) and cetaceans (Giménez *et al.*, 2017; Marçalo *et al.*, 2018). Both fish species have significant economic value worldwide, including in the oceanic region of Madeira, where an average of 400 and 200 tonnes (2008-2018, DRPM, Unpublished data) of *T. picturatus* and *S. colias*, respectively, are fished every year. These species also have important roles in the tuna fishing activities as bait (Hermida and Delgado, 2016; Tejerina *et al.*, 2019).

Because of the importance of both mackerel species in fisheries, several studies have focused on several aspects of their ecology, like stock assessment, life history parameters, reproduction and trace elements (Garcia *et al.*, 2015; Lozano-Bilbao *et al.*, 2019; Raimundo *et al.*, 2013; Vasconcelos *et al.*, 2006, 2011, 2012). However, there is still limited knowledge on their feeding ecology (e.g. Bachiller and Irigoien, 2015; Garrido *et al.* 2015; Wahbi *et al.*, 2015) and few studies were carried out in oceanic environments (Castro, 1993; Denda *et al.*, 2017; Hirch and Christiansen, 2010). To date there are no detailed studies on the diet of these two species in the vast oceanic area that surrounds the archipelago of Madeira. Such information may provide an insight on the planktonic communities of this poorly known ecosystem and allows to better understand what sustains the pelagic trophic web of this region.

The main goal of this study is to describe the diet of the *S. colias* and the *T. picturatus* in the oceanic region of Madeira, and its seasonal variability throughout the

year. Based on the analysis of stomach contents and the use of stable isotope analysis of Carbon and Nitrogen, we (1) identify the most important prey for each species in overall and in each season, (2) describe their trophic position, and (3) compare the diet of the two mackerel species.

Methods

Ethical Statement

The fish analysed in this study were acquired dead by the Madeira Regional Fisheries Directorate (DRP), under the framework of the Programa Nacional de Recolha de Dados da Pesca (multiannual European Union programme for the collection, management and use of data in the fisheries and aquaculture sectors).

Sampling

Between February 2017 and January 2018, *S. colias* and *T. picturatus* individuals were obtained from commercial landings of local purse-seine fishing vessels (mostly using an 18mm mesh size), operating south of Madeira Island. A total of 20 individuals of each species were collected every month, except in July, August and December (for both species), and November (for the *T. picturatus*) (see Supporting Information, Table S1). For each individual, we recorded the total length (see Supporting Information, Table S1), total mass, mass of the stomach and of its content, and also of the gonads (IPIMAR, 2009).

Stomach contents analysis

To avoid variability in dietary data due to ontogenetic differences, we selected individuals of each species belonging to the modal size classes of 20-24 cm and 19-22 cm for *S. colias* and *T. picturatus*, respectively, for each month. In June (for *S. colias*) and September (for *T. picturatus*) there were not enough individuals within the selected size range. Therefore, we sampled nine S. *colias* of 22-27 cm, and four *T. picturatus* of 15-20 cm.

Sampling followed the procedures described in Garrido *et al.* (2015). We carefully collected the entire content of the cardiac and pyloric regions, to avoid food items in more advanced stages of digestion in the intestine. For both species, groups of stomach contents from 3 individuals collected in the same haul were combined to form a single sample, and an aliquot was used to identify and count prey items. Stomach samples were filtered using a 200 µm sieve (see Supporting Information, Table S2,). Fractions <200 µm were homogenized, placed in a Utermhol chamber and identified using an inverted microscope

(Leica DM IL LED) at a magnification of 200x. Fractions >200 µm were homogenized in a known volume of water and analysed under a stereomicroscope at a magnification of 160x (Olympus SZX12). Since *T. picturatus* is not a consumer of phytoplankton (e.g. Hirch and Christiansen, 2010; Kompowski, 1976), this group was only quantified in the stomachs of *S. colias*. All food items were identified to the lowest possible taxonomic level. Fish scales found in the stomachs of both mackerel species were disregarded, as they were most probably swallowed during the fishing event (Hernández and Ortega, 2000; Hirch and Christiansen, 2010; Kompowski, 1976).

Diet characterization

To assess the percentage of empty stomachs of each species, we calculated the vacuity index as the number of empty samples in relation to the total number of samples of each species. The feeding intensity (FI%) of both mackerel species, used to assess the stomach fullness, was calculated as:

$$FI\% = \frac{stomach\ content\ mass}{total\ mass - gonads\ mass} \times 100$$

To describe the diet of the *S. colias* and the *T. picturatus*, we calculated the frequency of occurrence (FO%), as the number of samples in which a prey group occurred in relation to the total number of samples. To account for the importance of prey for dietary energy we estimated the contribution of prey to dietary carbon by estimating the percentage of carbon content (CC%) as the mass of carbon of each prey group in the sample in relation to total dietary carbon in that sample. The carbon content of each prey was calculated using published relationships of volume and weight with their carbon content of phytoplankton, zooplankton and ichthyoplankton organisms (see Supporting Information, Table S3). To assess the importance of each prey in the diet of the two mackerels, the modified index of relative importance (mIRI) was calculated according to the equation (Hayse, 1990):

$$mIRI = FO\%\ of group\ prey \times CC\%\ of group\ prey$$

The diversity of the diet of the two mackerel species was compared using the Shannon-Wiener index, based on the mean percentage of carbon content of each prey (lowest taxonomic level identified). To avoid bias due to the different number of samples collected for each species (n=22 and n=27, for *T. picturatus* and *S. colias*, respectively), and to estimate the variability within each species, we calculated the means and standard deviations of 1000 random samples (with repetition) of n=22 from each species. Dietary

overlap between *S. colias* and *T. picturatus* was calculated using the Schoener's index, based on the carbon contribution of each prey (S):

$$S = 1 - 0.5(\sum_{i=1}^{n} | C_{ij} - C_{ik} |)$$

C_{ij} and C_{ik} are the proportion of carbon content of prey *i* (lowest taxonomic level identified) in the diet of species *j* and species *k*. The index varies between zero (diets are completely different) and one (identical proportions of all prey) and values >0.6 are considered to represent a significant diet overlap (Wallace and Ramsey, 1983).

The temporal variability of diet content was assessed by dividing the year in four seasons: Season 1 (February-April), Season 2 (May-July), Season 3 (August-October) and Season 4 (November-January). For each season, the relative importance of each prey based on the carbon content contribution was calculated, such as the frequency of occurrence and mIRI. Differences in prey groups (%CC) among seasons were described using multivariate ordination (Principal Component Analysis, PCA).

Stable isotope analysis

White muscle of *S. colias* (n=12) and *T. picturatus* (n=12) individuals was collected for nitrogen and carbon stable isotope analysis. Before analysis, samples were lipid-extracted using a chloroform-methanol (2:1) solution. The analysis was performed using a continuous-flow isotope-ratio mass spectrometer (CF-IRMS) on a Sercon Hydra 20-22 (Sercon, UK) coupled to a EuronEA (EuroVector, Italy) elemental analyser, which automatizes the samples preparation (Preston and Owens, 1983), in the Stable Isotopes and Instrumental Analysis Facility of the University of Lisbon. The results are expressed relative to atmospheric nitrogen for δ^{15}N, and the Vienna Pee Dee Belemnite for δ^{13}C. The precision of the analysis was calculated using values from six to nine replicates of laboratory standard material (casein), ≤0,08‰ for δ^{15}N and ≤0,06‰ for δ^{13}C.

To compare the isotopic niches of *S. colias* and *T. picturatus*, we estimated the corrected standard ellipse area (SEA*c*) of each species corresponding to 95% of the data and the overlap of these ellipses using the function *maxLikOverlap* of the *SIBER* R package (Jackson *et al.*, 2011). The proportion of the overlapping area was calculated as the ratio of the overlap area with the total area of the two polygons minus the overlap area (or with the area of the polygon of each mackerel). The trophic position (TP) of the consumers was estimated from the isotopic ratios according to Vander Zanden and Rasmussen (2001):

$$TP = TP_b + (\delta^{15}N_c - \delta^{15}N_{base})/\Delta N$$

where TP_b is the baseline of the trophic web (in this case, Particulate Organic Matter (POM)=1.5), $\delta^{15}N_c$ is the $\delta^{15}N$ of the consumer, and $\delta^{15}N_{base}$ is the mean $\delta^{15}N$ of POM. ΔN is the enrichment in ^{15}N per trophic level and was assumed to be 3.4% (Post, 2002). All analyses were performed using R version 3.5.2 (R Core Team, 2018).

Results

Overall diet

A total of 27 samples, pooled from 81 stomachs of *S. colias* were analysed, none of which was empty. From these, 66 prey types, belonging to 41 orders, were identified (Table 1). For *T. picturatus*, 22 samples pooled from 66 stomachs were analysed, with a vacuity index of 4.6%. Twenty-eight prey types, belonging to 15 orders, were described for this species (Table 1). In general, *S. colias* presented a more diverse diet (Shannon-Wiener index: *S. colias* =2.6±0.2 (SE) and *T. picturatus* =2.3±0.1) and higher feeding intensities (FI%=1.1, range=[0.6-2.0]) than the *T. picturatus* (FI%=0.3 [0.2-0.4]).

In this study, *S. colias* fed on phytoplankton, zooplankton, fish, cephalopods, and tunicates, and *T. picturatus* fed on zooplankton and fish. Overall, fish represented the highest mean contribution to *S. colias* dietary carbon (51.5±48.2% (SD), n=22), slightly higher than zooplankton (36.3±45.6%), while the pattern was inversed in terms of frequency of occurrence (100% for zooplankton vs. 66% for fish). Contrarily, for *T. picturatus*, zooplankton presented the highest mean contribution to dietary carbon (63.6±49.2%, n=27) and was present in more stomachs (FO%=95%), followed by fish (%CC=31.8±47.7% and FO%=31%). The mIRI was higher for zooplankton than for fish in the diet of both species due to the lower frequency of occurrence of fish in the stomachs (Table 1). *Scomber colias* occasionally included small cephalopods in their diet (FO% ca. 15%), a food item which was not detected in the diet of *T. picturatus*.

Both mackerel species preyed mainly on copepods, which was the most important group among planktonic crustaceans, both in frequency of occurrence and carbon content (Table 1). Among these, calanoids (*Candacia* sp. and *Pleuromamma* sp.) and unidentified copepods were the dominant prey and the ones with the highest mIRI (Table 1). Cyclopoid copepods (*Oncaea* sp.) were also consumed, occurring more frequently in the *S. colias* diet than in *T. picturatus*. Crustacean decapods and pteropods (Gastropoda) were also important in the diet of *T. picturatus*. Eggs of crustaceans, fish and gastropods were

frequently found in the stomachs of *S. colias* and represented on average 1.2±0.8% of contribution to dietary carbon.

Despite being present in all *S. colias* stomachs analysed, the carbon contribution of phytoplankton (1.4±4.5%) was very low, mostly comprising dinoflagellates (*Dinophyceae*) and diatoms (*Pennales, Achnanthales*).

Atlantic saury *Scomberesox saurus* Walbaum 1792 and Longspine snipefish *Macroramphosus scolopax* Linnaeus 1758 were the most important fish prey identified in the diet of *S. colias* and *T. picturatus*, respectively. Cannibalism was observed in 11% of the samples of *S. colias* analysed and represented the second most important fish contribution to its diet.

Seasonal variation

In Season 1, *S. colias* consumed the highest variety of prey, including unidentified fish and crustaceans, among them decapods and copepods (calanoids: *Candacia* sp. and *Euchaeta* sp., and cyclopoids: *Oncaea* sp. and *Corycaeus* sp.) (Table 1). In Season 2 Clupeidae and unidentified fish were the most important for the diet of *S. colias* as well as copepods (*Candacia* sp., *Corycaeus* sp., *Scolecithrix* sp. and *Sapphirina* sp.). In Season 3, fish dominated the diet of *S. colias* (*M. scolopax, S. colias, S. saurus* and other unidentified species), as in Season 4 (unidentified, European pilchard *Sardina pilchardus* Walbaum 1792 and *S. colias),* in which copepods were also important (*Candacia* sp., *Corycaeus* sp. and *Pleuromamma* sp.). The carbon content of cephalopods in the stomachs of S. colias were highest in Season 4 (Table 1).

For *T. picturatus*, Season 1 was characterized by higher consumption of myctophids and other unidentified fish, crustaceans (among them calanoids and other copepods, Brachyura and Anomura), and pteropods (Table 1). In Season 2, unidentified fish, pteropods, copepods, among them *Candacia* sp., and other crustaceans were the most consumed. Season 3 was dominated by decapods, including Anomura, fish, namely *M. scolopax,* and copepods, namely *Pleuromamma* sp.. In season 4, the most important prey of *T. picturatus* were crustaceans, with copepods like *Candacia* sp. and *Pleuromamma* sp. representing the bulk of its diet.

The multivariate ordination (PCA) of prey groups showed higher differentiation in the prey consumed between each season than between each mackerel species (Figure 1). For *S. colias,* Seasons 3 and 1 were the most different amongst each other and Season 2 and 4 were the most similar, being these last two differentiated from the other seasons

by a higher consumption of crustacean eggs, cephalopods and fish. Seasons 1 and 3 are more segregated due to the consumption of a more varied set of prey in the former, and fish in the latter. For *T. picturatus*, Seasons 3 and 4 were the most different, while Season 1 and 2 the most similar. Seasons 1 and 2 are different from other seasons due to a higher consumption of decapods and gastropods. Season 3 was characterized by a higher consumption of decapods and fish, while Season 4 was distinct due to *T. picturatus* consuming more copepods and other crustaceans.

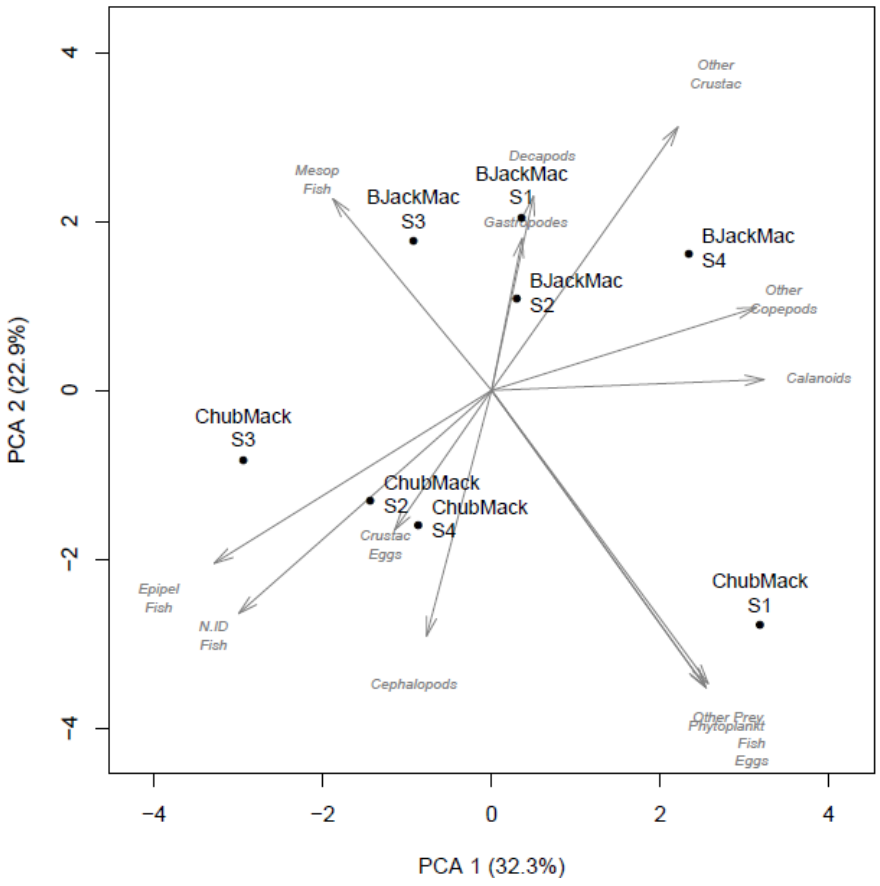


Figure 1 – Principal component analysis (PCA) of the percentage of carbon contribution of prey and their predators, Atlantic chub mackerel *Scomber colias* (ChubMack) and Blue jack mackerel *Trachurus picturatus* (BJackMac), per season (S1: February-April, S2: May-July, S3: August-October, S4: November-January). Prey were grouped in Epipelagic fish (Epipel Fish), Unidentified fish (N. ID. Fish), Crustacean eggs (Crustac Eggs), Cephalopods, Other Prey, Phytoplankton, Fish Eggs, Calanoids, Other Copepods, Other Crustaceans (Other Crustac), Decapods, Gastropods, Mesopelagic Fish (Mesop Fish).

Trophic levels and Isotopic niches

There was a significant difference between the $\delta^{15}N$ isotopic ratios of both mackerel species, 9.6±0.2 (SD)‰ and 8.6±0.7‰ for *T. picturatus* and *S. colias*, respectively (ANOVA: $F_{1,22}$=24.3, *P*<0.001). Conversely, $\delta^{13}C$ ratios were not significantly different, -19.9±0.4‰ and -20.0±0.5‰ for *T. picturatus* and *S. colias*, respectively ($F_{1,22}$=0.364, *P*=0.55). The estimated trophic levels were significantly different ($F_{1,22}$=24.3, *P*<0.001) for the two mackerel species, 3.09±0.05 and 2.78±0.21 for *T. picturatus* and *S. colias*, respectively. The isotopic niche of *T. picturatus* was smaller than that of *S. colias* (*T. picturatus* isotopic area: 1.4 and *S. colias* isotopic area: 5.7; *P*=0.99; Figure 2). The total dietary overlap in the isotopic space was 16%, which agrees with the value of Schoener's index, estimated at 0.51. The dietary overlap for the *S. colias* corresponded to 17% and for the *T. picturatus* 70% (Figure 2).

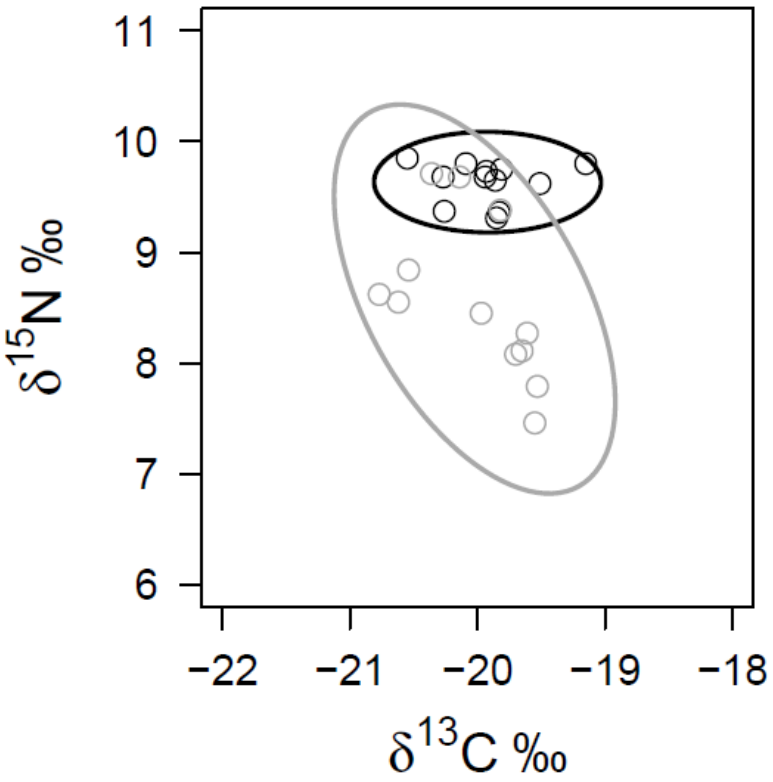


Figure 2 – Standard ellipse areas (SEAc, 95%) of individual Atlantic chub mackerel *Scomber colias* (in grey) and Blue jack mackerel *Trachurus picturatus* (in black) sampled in the archipelago of Madeira between February 2017 and January 2018.

Table 1 - Diet composition of Atlantic chub mackerel *Scomber colias* and Blue jack mackerel *Trachurus picturatus* captured in the archipelago of Madeira, per season (Season 1: February-April; Season 2: May-July; Season 3: August-October; Season 4: November-January) and annual.

Prey	*Scomber colias*										*Trachurus picturatus*									
	Season 1		**Season 2**		**Season 3**		**Season 4**		**Annual**		**Season 1**		**Season 2**		**Season 3**		**Season 4**		**Annual**	
	%CC†	**mIRI‡**	**%CC**	**mIRI**	**%CC**	**mIRI**	**%CC**	**mIRI**	**%CC**	**mIRI**	**%CC**	**mIRI**	**%CC**	**mIRI**	**%CC**	**mIRI**	**%CC**	**mIRI**	**%CC**	**mIRI**
Phytoplankton	**3.8**	**382.7**	**0.3**	**29.7**	**<0.1**	**0.4**	**0.2**	**15.9**	**1.4**	**137.8**										
Diatoms	**0.3**	**27.2**	**<0.1**	**0.2**	**<0.1**	**<0.1**	**<0.1**	**0.7**	**<0.1**	**9.3**										
Bacillariophyceae	0.2	18.0	<0.1	0.2	<0.1	<0.1	<0.1	0.2	<0.1	5.4										
Achnanthales																				
Achnanthes sp.	<0.1	1.6							<0.1	0.2										
Cocconeis sp.							<0.1	<0.1	<0.1	<0.1										
Pennales	0.1	7.4	<0.1	<0.1	<0.1	<0.1	<0.1	0.4	<0.1	2.5										
Chlorophyta																				
Pyramimonadales																				
Pyramimonas sp.	<0.1	3.7	<0.1	0.3					<0.1	0.8										
Coccolithophores	**0.2**	**13.5**			**<0.1**	**0.1**	**<0.1**	**1.1**	**<0.1**	**3.8**										
Dinoflagellates	**2.7**	**274.9**	**0.3**	**28.5**	**<0.1**	**0.4**	**0.1**	**13.9**	**1.0**	**101.1**										
Dinophyceae																				
Dinophysiales																				
Dinophysis sp.			<0.1	0.3					<0.1	<0.1										
Gonyaulacales																				
Gonyaulax sp.					<0.1	<0.1			<0.1	<0.1										
Lingulodinium polyedra	<0.1	4.1							<0.1	0.5										
Gymnodiniales																				
Gymnodinium sp.			<0.1	0.1					<0.1	<0.1										
Peridiniales																				
Protoperidinium sp.			<0.1	1.4					<0.1	<0.1										
Scrippsiella sp.	<0.1	3.6							<0.1	0.4										
Prorocentrales																				
Prorocentrum sp.									<0.1	<0.1										
Cyst dinoflagellates	0.5	48.5	<0.1	2.6	<0.1	<0.1			0.2	12.4										
Unidentified	2.2	217.7	0.2	24.0	<0.1	0.3	0.1	13.9	0.8	81.1										

Unidentified phytoplankton	0.6	61.3	<0.1	0.7					0.2	11.4									
Zooplankton	**73.4**	**7341.5**	**19.7**	**1966.9**	**0.3**	**31.2**	**33.3**	**3330.6**	**36.3**	**3631.4**	**55.6**	**4940.7**	**66.7**	**6667.5**	**66.7**	**6666.8**	**99.9**	**9999.9**	**63.6**	**6075.6**
Crustacea																			
Hexanauplia																			
Copepoda (subclass)	44.0	4400.8	14.6	1463.2	<0.1	8.5	30.6	3059.5	24.7	2473.9	18.3	101.6	32.2	2147.4	19.4	1296.1	84.6	8460.6	29.6	1881.1
Calanoida									14.1	1253.6									13.5	612.6
Acartia sp.	0.1	1.0					<0.1	<0.1	<0.1	0.2										
Calanus helgolandicus	2.6	28.8	<0.1	0.2			1.0	16.4	1.1	12.1										
Paracalanus sp.			<0.1	<0.1					<0.1	<0.1										
Candacia sp.	14.2	948.2	3.9	391.4	<0.1	1.8	7.3	729.6	7.2	616.5	<0.1	<0.1	5.8	96.0	1.8	89.2	15.9	1061.3	3.9	88.7
Chirundina sp.															0.7	33.6			<0.1	0.3
Eucalanus sp.	0.6	6.8							0.2	0.8										
Euchaeta sp.	3.4	112.8							1.1	12.5			3.9	65.1					1.1	4.8
Heterorhabdus papilliger			0.3	21.1					<0.1	1.0										
Mesocalanus tenuicornis							<0.1	<0.1	<0.1	<0.1			<0.1	0.1					<0.1	<0.1
Metridia sp.	1.0	11.0							0.3	1.2										
Pleuromamma sp.			<0.1	0.1	<0.1	0.4	7.2	598.2	1.6	53.3					13.4	671.3	25.8	1719.7	4.7	64.6
Scolecithrix sp.			3.4	283.5	<0.1	<0.1	0.4	17.8	0.8	27.8					0.6	38.1	4.4	145.9	0.7	8.8
Temora longicornis							<0.10	0.1	<0.1	<0.1										
Temora stylifera	0.4	8.2					1.1	52.9	0.4	6.6	0.3	3.4							0.1	0.5
Unidentified	3.4	113.0	<0.1	0.1	<0.1	0.1	0.4	6.8	1.2	31.7	7.2	159.4							2.9	26.7
Cyclopoida									4.1	414.8									1.9	71.5
Corycaeus sp.	1.9	129.3	1.4	120.4	<0.1	2.3	3.9	327.9	1.8	150.5			3.2	53.2					0.8	3.9
Oithona sp.	0.1	0.7	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	0.6							0.1	4.5	<0.1	<0.1
Oncaea sp.	4.2	422.2	0.9	90.1	<0.1	0.5	0.5	48.3	1.7	171.6	0.5	17.5	2.9	95.7			<0.1	0.6	0.9	27.3
Sapphirina sp.			1.6	137.0			0.9	29.9	0.6	14.6					0.9	42.8			<0.1	0.4
Harpacticoida	<0.1	<0.1	0.1	1.9	<0.1	0.7	1.2	58.5	0.3	11.2										
Unidentified Copepoda	12.1	1212.2	2.9	293.6	<0.1	1.0	6.8	682.6	6.2	621.2	10.3	571.7	16.5	1098.3	2.1	106.5	38.4	3836.2	14.1	834.8
Cirripedia (Infraclass)			<0.1	<0.1					<0.1	<0.1										
Malacostraca	**11.6**	**513.5**	**1.0**	**54.5**	**0.2**	**20.7**	**<0.1**	**2.0**	**4.1**	**245.8**	**15.9**	**528.4**	**<0.1**	**0.1**	**45.0**	**3753.3**	**3.8**	**127.0**	**14.1**	**513.8**
Amphipoda	0.8	18.1	<0.1	<0.1	<0.1	1.1	<0.1	0.2	0.3	10.3	<0.1	<0.1			2.9	145.2			0.3	2.4
Decapoda	8.7	291.1	<0.1	0.4	0.1	5.1			2.9	86.9			<0.1	0.1	27.1	2259.1	3.8	127.0	6.0	136.7
Brachyura (Infraorder)	2.0	66.4	1.1	35.6	<0.1	0.7			0.9	30.1	9.2	102.6			1.1	54.8			3.9	35.2

Anomura (Infraorder)					0.1	6.5	<0.1	0.6	<0.1	0.6	6.6	73.4			13.9	696.5			3.9	36.1
Isopoda					<0.1	0.1			<0.1	<0.1										
Mysida	<0.1	0.3							<0.1	<0.1										
Ostracoda			**0.1**	**2.0**					**<0.1**	**0.1**										
Crustacea eggs	**5.4**	**120.2**	**<0.1**	**0.1**	**<0.1**	**<0.1**	**0.6**	**30.0**	**0.8**	**78.7**	**<0.1**	**0.6**	**<0.1**	**2.2**	**<0.1**	**0.6**	**<0.1**	**1.2**		
Copepoda eggs	<0.1	<0.1	<0.1	<0.1			<0.1	<0.1	<0.1	<0.1										
Unidentified eggs	<0.1	1.1	3.1	307.9	<0.1	<0.1	0.4	44.7	0.8	78.7	<0.1	0.6	<0.1	2.2	<0.1	0.6	<0.1	1.2	<0.1	1.5
Unidentified Crustacea	**3.3**	**334.4**	**0.5**	**47.6**	**<0.1**	**0.8**	**0.7**	**67.9**	**1.4**	**137.3**	**15.0**	**998.4**	**3.1**	**204.3**	**1.0**	**80.1**	**10.9**	**1093.5**	**8.5**	**621.2**
Bivalvia	**<0.1**	**<0.1**	**0.2**	**7.6**	**<0.1**	**0.1**	**<0.1**	**<0.1**	**<0.1**	**1.0**	**<0.1**	**<0.1**							**<0.1**	**<0.1**
Gastropoda	**<0.1**	**<0.1**	**<0.1**	**<0.1**	**<0.1**	**0.6**	**<0.1**	**<0.1**	**6.3**	**347.4**	**31.3**	**3133.0**	**1.2**	**81.2**	**0.6**	**20.2**	**0.6**	**20.2**		
Pteropoda			<0.1	<0.1	<0.1	0.6	<0.1	<0.1	<0.1	<0.1	5.8	324.7	28.2	2823.5	1.2	81.2	0.6	20.2	10.3	654.5
Gastropoda eggs	**0.4**	**19.6**	**0.1**	**5.2**	**<0.1**	**<0.1**	**<0.1**	**<0.1**	**0.2**	**8.9**	**0.2**	**4.3**					**<0.1**	**0.8**	**<0.1**	**1.1**
Unidentified Gastropoda	**<0.1**	**<0.1**							**<0.1**	**<0.1**	**0.4**	**4.5**	**3.1**	**51.6**					**1.0**	**9.1**
Fish eggs	**5.4**	**120.2**	**<0.1**	**0.1**	**<0.1**	**<0.1**	**0.6**	**30.0**	**1.9**	**57.4**										
Microzooplankton	**8.6**	**864.5**	**0.1**	**11.2**	**<0.1**	**0.2**	**0.9**	**94.4**	**3.1**	**300.2**										
Echinodermata (phylum)	**4.5**	**400.1**					**0.5**	**44.6**	**1.6**	**77.9**										
Foraminifera (phylum)	**0.2**	**14.3**							**<0.1**	**1.6**										
Radiozoa (phylum)			**<0.1**	**<0.1**					**<0.1**	**<0.1**										
Ciliophora (phylum)																				
Tintinnina (suborder)	4.0	354.0	0.1	11.2	<0.1	0.2	0.4	34.1	1.4	128.4										
Tunicata	**0.1**	**3.0**							**<0.1**	**0.3**										
Appendicularia																				
Copelata																				
Oikopleura sp.	0.1	1.5							<0.1	0.2										
Thaliacea																				
Salpida	<0.1	<0.1							<0.1	<0.1										
Teleostei	**18.9**	**421.9**	**58.3**	**3884.3**	**99.7**	**9967.2**	**45.2**	**2258.5**	**51.5**	**2859.1**	**33.3**	**1110.2**	**33.3**	**1110.8**	**33.3**	**1111.1**			**31.8**	**1011.9**
Epipelagic fish			**16.6**	**276.7**	**66.4**	**4429.3**	**33.3**	**1108.7**	**25.8**	**670.0**					**28.6**	**954.2**			**7.8**	**70.9**
Clupeidae																				
Sardina pilchardus							16.7	277.6	3.7	13.7										
Unidentified			16.6	276.7					3.7	13.7					8.5	141.3			2.3	10.5
Centriscidae																				

Macroramphosus scolopax					16.6	276.7			3.7	13.7					20.1	671.6	5.5	49.9
Scombridae																		
Scomber colias					10.3	343.5	16.6	276.7	5.9	66.4								
Scomberesocidae																		
Scomberesox saurus					39.5	1976.6			8.8	97.6								
Mesopelagic fish					**<0.1**	**0.2**			**<0.1**	**<0.1**	**11.1**	**123.2**					**4.5**	**20.6**
Myctophidae					**<0.1**	**0.2**			**<0.1**	**<0.1**	**11.1**	**123.1**					**4.5**	**20.6**
Unidentified fish	**19.0**	**422.0**	**41.7**	**2083.2**	**33.2**	**1107.4**	**11.9**	**198.5**	**25.6**	**759.1**	**22.2**	**493.8**	**33.3**	**1110.8**	**4.7**	**78.4**	**19.5**	**442.3**
Cephalopoda																		
Unidentified Cephalopoda	**3.2**	**35.1**	**8.1**	**135.6**			**21.3**	**710.0**	**7.6**	**112.5**								

Discussion

This work is the first to describe the diet of *S. colias* and *T. picturatus* in the archipelago of Madeira. It also provides novel data on the zooplanktonic communities in this poorly known oceanic region of the Atlantic. The size classes analysed in this study correspond to a narrow size class range (modal size class in the fishery), which excludes ontogenetic variations of the diet. Our data showed that both species fed on planktonic and micronektonic prey from the epipelagic environment, with a modest contribution of mesopelagic prey. A seasonal variation was observed in both mackerel's diet which seems to be related to the availability of fish and cephalopods, temporarily replacing the smaller sized planktonic species. *S. colias* fed on a wider variety of prey than *T. picturatus*, which overall resulted in moderate overlap in their diet compositions and isotopic niches.

Around Madeira, the diet of *S. colias* suggests that this species is an opportunistic forager, while *T. picturatus* showed to have a more selective diet that incorporates larger prey and a higher degree of piscivory. These results agree with other studies in the Mediterranean (Battaglia *et al.*, 2019; Sever et al., 2006), subtropical and tropical eastern Atlantic (Castro and Santana del Pino, 1995; Denda *et al.*, 2017; Gushchin and Corten, 2017; Kompowski, 1976) and Iberian coast (Bachiller and Irigoien, 2015; Garrido *et al.*, 2015). The wider prey variety presented by the *S. colias* has been previously described (Bachiller and Irigoien, 2015) and is most probably related to a higher ability of the feeding apparatus to retain smaller prey and an eventual filter-feeding behaviour (Costalago *et al.*, 2015). This opportunistic feeding behaviour may explain the more diverse diet found in this study than in studies conducted in other regions (e.g. Castro and Santana del Pino, 1995; Garrido *et al.*, 2015; Wahbi *et al.*, 2015).

Among the planktonic prey, calanoid copepods were the most consumed by both mackerel species in this study, but this is also true in other studies performed in the Portuguese coast (Garrido *et al.*, 2015) and the Àmpere seamount (Denda *et al.*, 2017), for example. Mysids and euphausiids, which had important roles in the diet of these mackerels in other regions (Bachiller and Irigoien, 2015; Battaglia *et al.*, 2019; Castro, 1993; Kompowski, 1976; Sever *et al.*, 2006;), and in a previous study conducted in Madeira (Costa *et al.*, 2013), were infrequent in our study. The differences found between Costa *et al.* (2013) and our study suggests long-term changes in the abundance of those species in the Madeira oceanic region, suggesting the existence of a dynamic planktonic community.

Fish was an important prey in the diet of *S. colias* and *T. picturatus* around the Madeira waters, alongside zooplanktonic species. To the best of our knowledge, this was only described for *S. colias* in two other studies off Mauritania and Turkey coasts (Gushchin and Corten, 2017; Sever *et al.*, 2006), as fish are often reported having little importance in the Atlantic and in the Mediterranean. Species such as *M. scolopax*, *S. pilchardus*, myctophids (Castro, 1993; Denda *et al.*, 2017; Gushchin and Corten, 2017; Sever *et al.*, 2006; Wahbi *et al.*, 2015), and *S. saurus* (this study) can be found in mackerel's stomachs in these regions. Our results also contrast with data obtained in the Portuguese coast, where both mackerel species have a strictly planktonic diet (Garrido *et al.*, 2015). Although the slightly lower average size of the *T. picturatus* analysed in Garrido *et al.* (2015) (ca.18 cm, total length) might contribute to partly explain the difference in diet, as younger individuals tend to consume smaller crustaceans, like copepods, euphausiids and decapod larvae (Kompowski, 1976), the same does not hold for *S. colias*. It is possible that the disparity found in the diet of the *S. colias* in different regions is linked to its opportunistic behaviour (Hernández and Ortega, 2000) and to different prey communities in different areas.

Cannibalism has been previously reported in *S. colias* and other pelagic forage fish, such as *S. pilchardus* (Castro, 1993; Garrido *et al.*, 2008), supporting the same conclusions reached for *S. colias* in this study. On the other hand, this was not observed for *T. picturatus* here, which consumed mainly *M. scolopax* and myctophids, following the results found in other studies (Battaglia *et al.*, 2019; Hirch and Christiansen, 2010). Unlike what has been reported in other studies of individuals of similar sizes (e.g. Battaglia *et al.*, 2019; Kompowski, 1976), cephalopods were not consumed by *T. picturatus* in our study. The reasons for this behaviour remain unclear, as cephalopods are diverse and abundant in this region (Hastie *et al.*, 2009).

This study found seasonal variations in the diets of the *S. colias* and *T. picturatus*. Zooplanktonic (and also phytoplanktonic for *S. colias*) species were constantly present in the stomachs of both mackerels, which indicates that they comprise the base of the diet for these species, being available all year round. Although planktonic species are easier to capture, their caloric content is lower than that of bigger more nutritious prey, which, on its turn, also require more energy to be preyed. Here, we hypothesise that the seasonal differences observed in the diet of these two mackerel species are directly linked to the abundance of planktonic species and the abundance of fish and cephalopods. Mackerels may choose their prey to fit the best energetic balance.

While the two mackerel species fed on similar prey types, there was a wider range of different prey types in the diet of *S. colias* than in the diet of *T. picturatus*, resulting in differences in the index of dietary diversity. These differences in the relative importance of different prey also resulted in a low dietary overlap from the point of view of the *S. colias*, and in the smaller isotopic niche of the *T. picturatus*. This difference in the diet is further noticeable in their trophic levels, which is significantly higher in the *T. picturatus* than in the *S. colias*. In general, *S. colias* seem to have consumed more fish but also ingested phytoplankton, which can reduce their trophic level. This opportunistic behaviour likely confers an advantage for *S. colias*, which are able to prey on a higher diversity of prey sizes and prey types in this oligotrophic environment. Such species, like these mackerels, are excellent indicators of the existing planktonic communities (Reid *et al.*, 2001). Further studies on their seasonal variations may shed more light on the communities comprising the base of oceanic food webs like the pelagic ecosystem of the archipelago of Madeira.

Acknowledgements

This work was supported by Fundação para a Ciência e a Tecnologia (FCT Portugal) through the project Oceanwebs (PTDC/MAR-PRO/0929/2014), the strategic projects UIDB/04292/2020 and UIDP/04292/2020 granted to MARE, and UIDB/50017/2020 and UIDP/50017/2020 granted to CESAM. This study was partially supported by the Oceanic Observatory of Madeira Project (M1420-01-0145-FEDER-000001-Observatório Oceânico da Madeira-OOM). PD/BD/127810/2016 was granted to JR by FCT. MH was supported by a postdoctoral grant from ARDITI (Agência Regional para o Desenvolvimento da Investigação, Tecnologia e Inovação), Project M1420-09-5369-FSE-000001. Thanks are due to Fátima Quintela and Alexandra D. Silva for helping with zooplankton and phytoplankton identification, respectively.

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Supporting Information

Table S1 - Number of individuals collected for each month and species (Blue jack mackerel *Trachurus picturatus* and Atlantic chub mackerel *Scomber colias*) in the south of Madeira island, between February 2017 and January 2018, and respective range of total lengths.

	Scomber colias		***Trachurus picturatus***	
Date	**N**	**TL**[†]	**N**	**TL**
February 2017	20	24.3±1.8 (20.5-27.9)	20	22.2±1.3 (19.8-24.6)
March 2017	20	21.3±1.2 (19.6-23.6)	20	20.3±1.2 (18.7-24.5)
April 2017	20	22.4±0.9 (20.9-24.2)	20	19.5±0.6 (18.6-20.6)
May 2017	21	21.0±1.9 (18.3-25.2)	19	19.8±0.7 (18.4-21.0)
June 2017	20	25.3±1.3 (22.6-27.1)	20	20.2±0.8 (18.7-21.6)
September 2017	23	20.0±2.2 (17.2-24.6)	4	18.1±2.0 (15.3-19.6)
October 2017	20	22.6±1.7 (20.8-28.1)	20	19.9±1.7 (17.5-24.8)
November 2017	20	21.5±0.7 (20.4-22.5)	-	-
January 2018	20	23.6±0.9 (21.8-25.7)	20	19.6±1.0 (17.7-21.0)

[†]Total length

Table S2 - Number of stomachs analysed for each month and species (Blue jack mackerel *Trachurus picturatus* and Atlantic chub mackerel *Scomber colias*).

	Trachurus picturatus	*Scomber colias*	
Date	≥200µm	≥200µm	<200µm
February 2017	9	9	-
March 2017	9	9	3
April 2017	9	9	3
May 2017	9	9	3
June 2017	9	9	-
September 2017	3	9	3
October 2017	9	9	6
November 2017	-	9	-
January 2018	9	9	6
Total	66	81	24

Table S3 - Carbon content value of each prey item identified in the stomachs of the Atlantic chub mackerel *Scomber colias* and the Blue jack mackerel *Trachurus picturatus*, and references from which the data were obtained.

Prey	**Final Carbon content value (µg)**	**Mean length and mass reference**	**Reference**
Phytoplankton n.i.†	0,00145	-	(Garrido *et al.*, 2008)
Dinophyceae n.i.	0,00327	-	(Garrido *et al.*, 2008)
Dinophyceae cyst	0,00327	-	(Garrido *et al.*, 2008)
Dinophysis sp.	0,00495	-	(Garrido *et al.*, 2008)
Gonyaulax sp.	0,00536	(Espinoza & Bertrand, 2008)	(Espinoza and Bertrand, 2008)
Lingulodinium polyedra	0,00369	-	(Lewis and Hallett 1997)
Gymnodinium sp.	0,00225	-	(Menden-Deuer & Lessard, 2000)
Scrippsiella sp.	0,00123	-	(Garrido *et al.*, 2008)
Protoperidinium sp.	0,02257	-	(Garrido *et al.*, 2008)
Prorocentrum sp.	0,00205	-	(Garrido *et al.*, 2008)
Bacillariophyceae n.i.	0,00088	-	Mean values calculated from different prey from this study This study mean values
Pennales (Bacillariophyceae)	0,00072	-	(Garrido *et al.*, 2008)
Achnanthes sp.	0,00145	-	= Phytoplankton n.i.
Cocconeis sp.	0,00006	(Espinoza & Bertrand, 2008)	(Espinoza & Bertrand, 2008)
Pyramimonas sp. (Chlorophyta)	0,00145	-	= Phytoplankton n.i.
Coccolithophora sp.	0,00145	-	= Phytoplankton n.i.
Tintinnina n.i.	0,18062	-	(Garrido *et al.*, 2008)
Equinodermata n.i.	1,85000	Larvae 1mm; (Espinoza & Bertrand, 2008)	(Espinoza & Bertrand, 2008)
Foraminifera n.i.	0,01460	-	(Garrido *et al.*, 2008)
Radiozoa n.i.	0,00045	-	(Espinoza & Bertrand, 2008)
Crustacea n.i.	1,86038	-	(Garrido *et al.*, 2008)
Crustaceaeggs n.i.	0,01469	-	(Garrido *et al.*, 2008)
Crustaceaegglaying n.i.	0,86795	-	= Copepoda eggs
Copepoda n.i.	4,07082	-	(Garrido *et al.*, 2008)
Copepoda eggs	0,86795	-	(Garrido *et al.*, 2008)
Copepoda eggsack	0,01469	-	(Garrido *et al.*, 2008)
Calanoida n.i.	26,47974	-	Mean values obtained from Calanoid species detected in this study
Acartia sp.	4,02296	-	(Garrido *et al.*, 2008)
Chirundina sp.	26,47974	-	= Calanoida n.i.
Calanus helgolandicus	63,53851	-	(Garrido *et al.*, 2008)
Mesocalanus tenuicornis	26,47974	-	= Calanoida n.i.
Candacia sp.	23,42223	-	(Garrido *et al.*, 2008)
Eucalanus sp.	30,03926	-	(Garrido *et al.*, 2008)
Euchaeta sp.	37,00245	-	(Garrido *et al.*, 2008)

Heterorhabdus papilliger	26,47974	-	= Calanoida n.i.
Metridia sp.	48,66667	-	(Hopkins *et al.*, 1984)
Paracalanus sp.	14,85697	-	(Garrido *et al.*, 2008)
Pleuromamma sp.	22,02708	-	(Garrido *et al.*, 2008)
Scolecithrix sp.	22,49178	-	(Espinoza & Bertrand, 2008)
Temora longicornis	38,84597	-	(Garrido *et al.*, 2008)
Temora stylifera	6,27166	-	(Garrido *et al.*, 2008)
Corycaeus sp.	12,98689	-	(Garrido *et al.*, 2008)
Oithona sp.	0,93131	-	(Garrido *et al.*, 2008)
Oncaea sp.	0,63272	-	(Garrido *et al.*, 2008)
Sapphirina sp.	16,86000	TL‡ (Lopes *et al.*, 2007)	(Lopes *et al.*, 2007)
Harpacticoida n.i.	4,84607	-	(Garrido *et al.*, 2008)
Parasite Copepoda	4,07082	-	= Copepoda n.i.
Amphipoda n.i.	7,62509	-	(Garrido *et al.*, 2008)
Decapoda n.i.	137,116	-	(Garrido *et al.*, 2008)
Brachyura n.i.	43,14121	-	(Garrido *et al.*, 2008)
Anomura n.i. (Megalopslarvae)	137,116	CL§ = 1333µm; This study	(Nikolioudakis *et al.*, 2012)
Isopoda n.i.	80,000	-	(Elizalde *et al.*, 1999)
Mysida n.i.	60,15672	-	(Garrido *et al.*, 2008)
Ostracoda n.i.	2,55884	(ostracodjuvenile) = 6.035µg dm¶ (Borme *et al.*, 2009)	(Van Der Lingen, 2002)
Cirripedia n.i.	26,16838	-	(Garrido *et al.*, 2008)
Bivalvia	45,49852	TL= 1.25mm; (Espinoza & Bertrand, 2008) dm (James, 1987)	(Van Der Lingen, 2002)
Lamelibranchia veligera (Bivalvia)	6,13745	-	(Garrido *et al.*, 2008)
Cephalopoda	249260	TL = 8cm	(Espinoza & Bertrand, 2008)
Gastropoda n.i.	8,47578	-	(Garrido *et al.*, 2008)
Gastropoda egglaying	0,86795	-	= Copepoda eggs
Pteropoda	4,36044	-	(Garrido et al., 2008)
Appendicularia	5,80192	-	(Garrido *et al.*, 2008)
Salpidae	10,04400	L¥ = 6.2mm; Mean value of the maximum and minimum values (Heron *et al.*, 1988)	(Heron *et al.*, 1988)
Pisces n.i.	625610	-	Mean values of Pisces in this study
Pisces eggs	13,41405	-	(Garrido *et al.*, 2008)
Scomberesox saurus	480262	TL = 5cm	(Santos *et al.*, 2002)
Clupeidae n.i.	1126508	-	= *S. pilchardus*
Sardina pilchardus	1126508	TL = 8cm	(Coelho, 2009)
Scomber colias	1051304	TL = 8cm	(Vasconcelos et al., 2011)
Macroramphosus scolopax	462907	TL = 5cm	(Espinoza & Bertrand, 2008)
Myctophidae n.i.	7066,5	L = 2cm; (Espinoza & Bertrand, 2008)	(Froese, 1998)

† n.i.: not identified
‡ TL: Total length
§ CL: Carapace length
¶ dm: dry mass
¥ L: Length

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CHAPTER 3

Credits: Raquel Segur

This chapter is published as:

Joana Romero, Paulo Catry, Margarida Hermida, Verónica Neves, Bárbara Cavaleiro, Lídia Gouveia, José Pedro Granadeiro (2021). Tunas off northwest Africa: the epipelagic diet of the Bigeye and Skipjack tunas. Fisheries Research 238: 105914.

Tunas off northwest Africa: the epipelagic diet of the Bigeye and Skipjack tunas

Abstract

Tunas are among the most fished top predators worldwide, which has led to the depletion of many of their stocks. The decline of their populations has potentially great impacts in the food-web and the ecosystems. To better understand the impacts in the most important tuna areas, basic knowledge on the diet of these species in each region is required. Here, we describe the diet of the two most fished tuna species in the archipelago of Madeira, the Bigeye tuna *Thunnus obesus* and the Skipjack tuna *Katsuwonus pelamis*, based on stomach contents. To gain further insights into the diet, and also better assess the possible bias caused by the occurrence of live bait in stomachs, we compared tuna mercury values with those of two other predators with similar diets that are not directly targeted by fisheries. Bigeye tunas fed mostly on Atlantic chub mackerel *Scomber colias*, mackerel *Trachurus* sp. and Longspine snipefish *Macroramphosus scolopax*, also consuming some mesopelagic prey, including myctophids and cephalopods. Skipjack tunas had an epipelagic diet constituted mainly of Longspine snipefish and Sand smelt *Atherina* sp.. There were interannual variations in diet likely linked to interannual pelagic community shifts. Bait did not bias the results of the stomach analysis of these tunas and bait species were proved to be part of the natural diet of both tuna species. Baseline data provided by this study should allow for more informed decisions for an efficient ecosystem-based fisheries management.

Key words: *Thunnus obesus*, *Katsuwonus pelamis*, Diet, Mercury, Northeast Atlantic Ocean

Introduction

Marine top predators are among the most threatened functional groups in the wide ocean, with an estimated loss of biomass of large predatory fishes at around 90% in relation to pre-industrial numbers (Myers and Worm 2003). Among this group, tunas are one of the most targeted by the fishery industry. Every year, around half a million tonnes of tunas are captured worldwide (2000-2018; ICCAT 2020). Such pressure has led to the depletion of many stocks and, consequently, to the inclusion of several tuna species in the IUCN Red list of threatened species (IUCN 2020). Furthermore, the decline of top predators impacts the structure of communities and the diversity of food webs, as well as the productivity and connectivity of the ecosystems (Doney et al. 2012). Impacts are not only observed directly on their prey but can produce cascading effects on other marine species and communities. For example, the increase in tuna fishing activity in the 1960's in the eastern tropical Atlantic Ocean and the consequent decline of tuna populations in that area is thought to have caused a shift in the diet and a dramatic decline of the once massive Sooty tern *Onychoprion fuscatus* population of Ascension island which depends on interactions with sub-surface predators to locate and catch prey (Reynolds et al. 2019).

The Bigeye tuna *Thunnus obesus* (Vulnerable) and the Skipjack tuna *Katsuwonus pelamis* (Least concern) are the main targeted tuna species around the archipelago of Madeira (Gouveia et al. 2019), located in the subtropical NE Atlantic Ocean. In this archipelago there is a strong tuna fishing tradition taking place mostly from March to October (Gouveia and Mejuto 2003). Here tunas are caught mostly using pole-and-line, which uses small pelagic fish as live bait. In Madeira, an average of 1667 (±481 SD) and 549 (±461 SD) tonnes of Bigeye and Skipjack tuna, respectively, are landed every year (2007-2017; Gouveia et al. 2019), comprising an average of 35% of local fisheries landings and even reaching 50% in some years (Hermida and Delgado 2016).

Despite the considerable economic importance of tunas in the subtropical and temperate NE Atlantic, more specifically in Madeira, Azores and the Canary Islands, few ecological studies on these species have been conducted in this region. This contrasts with the various studies conducted in the Pacific on their distribution (eg. Houssard et al. 2019; Lehodey et al. 1997), movements (eg. Schaefer et al. 2009), reproduction (eg. Hunter et al. 1986), and contamination (eg. Chen et al. 2014), and also in the South and NW Atlantic (Matthews et al. 1977; Matsumoto and Miyabe 2002; da Silva et al. 2019). Large knowledge gaps on the ecology of these species remain in the Atlantic, such as migratory

routes, breeding periods and diet. To the best of our knowledge, a single study on the Skipjack tuna diet in the Canary Islands was published to this date (Ramos et al. 1995), and none on Bigeye tunas.

Tunas are opportunistic predators which means that their main prey shift according to region, reflecting prey availability in the different ocean compartments (Ménard et al. 2006; Gorni 2016; Ohshimo et al. 2018). Therefore, knowledge on their diet will contribute to our understanding of food web dynamics and allow to infer broad community-scale changes in the abundance, availability, and diversity of poorly known mid-trophic prey. Such knowledge is required for an ecosystem-based fisheries management and the conservation of large pelagic predators, including tunas.

Analysis of stomach contents is a direct and reliable way to thoroughly assess the diet of tunas (eg. Glaser et al. 2015; Varela et al. 2019). However, the use of live bait during fishing events may raise concerns about what proportion of stomach content is bait. Indirect techniques, like determination of mercury concentration in tissues have allowed to infer the diet of several predators for which sampling stomach contents is difficult (Layman et al. 2012; Teffer et al. 2014). Mercury concentrations can help distinguishing between a mesopelagic/bathypelagic diet and an epipelagic one, as deep-ocean species have significantly higher concentrations of mercury than epipelagic species due to the higher rate of microbial mediated methylation of mercury in sub-thermocline low oxygen waters (Choy et al. 2009).

The aim of this study is to describe the diet of two important top predators, the Bigeye and the Skipjack tunas, in the pelagic region around the Madeira archipelago, using stomach content analysis. To control for potential biases due to the use of live bait in this fishery, we also determined the mercury concentration in tissues of tunas and of two other abundant pelagic predators from the region with epipelagic diets, the Yellowmouth barracuda *Sphyraena viridensis* and the Longfin yellowtail *Seriola rivoliana*.

Methods

Tuna sampling

The stomachs of a total of 71 Bigeye tuna and 61 Skipjack tuna from a total of 16 and 10 fishing events, respectively, were obtained directly from local fishermen. Fish were captured using pole-and-line fishing vessels in Madeira island in 2016/2017 and 2016-2018 for Bigeye and Skipjack tuna, respectively. The individuals were measured

(±0.5cm), weighted (±1g), and the stomachs removed and kept frozen until sorting in the laboratory. A sample of blood was also collected for analysis of mercury concentration, and frozen until further processing in the laboratory. We obtained the coordinates of 22 tuna fishing events from local fishermen that took place in September 2017 and May-October 2018 which allowed us to produce an approximate map of the areas used for this fishing activity (Figure 1).

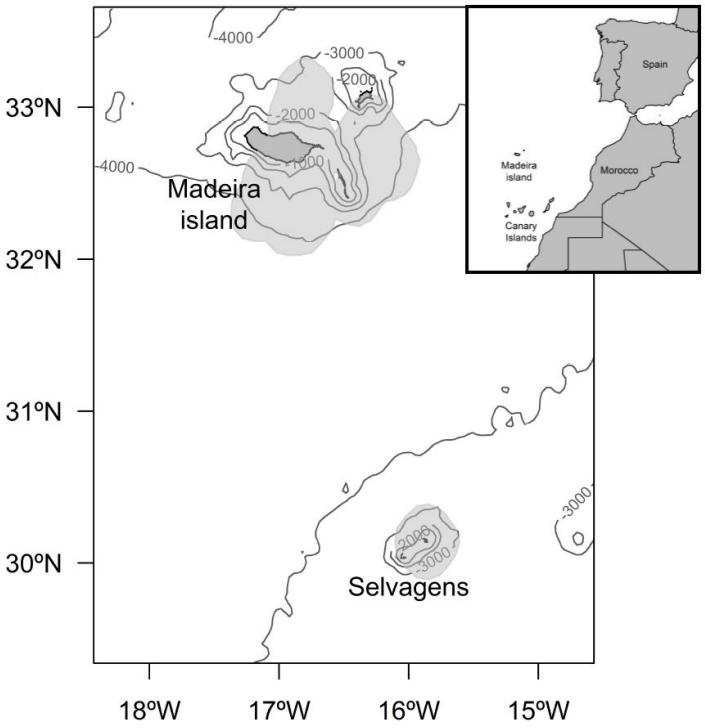

Figure 1 - Main areas (in grey) used by the tuna fishing vessels from Madeira island (95% Kernel Utilization Distribution). Areas were defined using coordinates of tuna fishing events in September 2017 and May-October 2018, as provided by fishermen (n=22). Isobathic lines of 1000, 2000, 3000, 4000m

Prey identification

Once in the laboratory, stomachs were thawed, and the contents carefully removed and classified according to digestion levels and type of prey (fish, cephalopods, crustaceans). Digestion levels for fish and cephalopods were attributed according to Aloncle and Delaporte (1974) and Alonso et al. (2018), respectively (Supplementary Material, Table A.1). Whenever the digestion level corresponded to I or II, fish prey were weighted (±0.1g), measured (±0.1cm) and identified using morphologic characteristics (Whitehead et al. 1989). Individuals with digestion levels of III or higher were identified using our reference collection of fish skeletons and otoliths from the NE Atlantic

(currently comprising over 700 specimens of ca. 100 species). Specific vertebrae were measured in order to obtain size estimations and weights of each individual (Granadeiro and Silva 2000). When identification using hard structures was not possible, a small piece of muscle was collected for DNA barcoding analysis. Cephalopods were identified using the lower beak (Clarke 1986; Lu and Ickeringill 2002) and DNA-barcoding analysis. Beaks with no tissue attached were excluded from the quantitative analysis due to the impossibility of knowing for how long they had been in the stomach. This way we avoid over-representation of cephalopod prey in the tuna's diet. The number of individuals in a sample was estimated by counting all identifiable structures. The Blue jack mackerel is the most common species of the genus *Trachurus* to be found in this marine region. However, due to the similarities of vertebrae between *Trachurus picturatus* and *Trachurus trachurus* and inability to confirm the exact species, we refer to this genus as *Trachurus* sp..

Tissues of 21 fish, 23 cephalopods and 6 crustaceans were sampled from stomach contents of Bigeye tuna and Skipjack tuna from which DNA was extracted using the E.Z.N.A. Tissue DNA kit (Omega Bio-tek). Optimized PCR conditions were used to amplify the 3' end region of the 16S rRNA gene of each prey DNA using the universal primers 16Sar and 16SSbr of Palumbi (1996) (Alonso et al. 2014). Both directions of the PCR products were sequenced in outsourcing (Macrogen Inc.). The resulting sequences were queried using BLAST (NCBI) and searches with similarity values higher than 98% were considered as positive identifications.

Diet characterization

The diets of Bigeye and the Skipjack tuna were characterized using numeric frequency (NF, number of individuals of a species in relation to the total number of individuals found in the stomachs) and frequency of occurrence (FO, number of stomachs in which a specific prey was found in relation to the total number of stomachs analysed). The Shannon-Wiener diversity index was used to calculate the prey diversity found in the stomachs of the two tuna species. Ontogenetic differences (length classes: 60-80, 80-100 and >100cm) in the diet of Bigeye tunas were assessed using Permutational multivariate analysis of variance (PERMANOVA).

Bait

In Madeira, Bigeye tuna's fishery involves the use of live bait to attract fish to the surface, particularly Atlantic chub mackerel *Scomber colias* and Blue jack mackerel

Trachurus picturatus. On the other hand, Skipjack tuna catches use European pilchard *Sardina pilchardus*, Sand smelt *Atherina* sp. or Bogue *Boops boops*, and when abundant, Longspine snipefish *Macroramphosus scolopax*.

Live bait has been considered a nuisance in diet studies of tuna due to the difficulty to distinguish it from the natural diet (Ankenbrandt 1985; Ramos et al. 1995). To address this issue, we (1) compared mercury concentrations in the tissues of the tunas studied with two other local predatory fishes known to have an epipelagic diet: Yellowmouth barracuda *Sphyraena viridensis* and Longfin yellowtail *Seriola rivoliana*; we also (2) excluded the bait (species known to be used as bait and with digestion levels I and II) from the original stomach content dataset and compared it with the diet inferred from the complete stomach content dataset (NF and FO) (Ankenbrandt 1985; Ramos et al. 1995).

Muscle samples of Yellowmouth barracuda and Longfin yellowtail were obtained from commercial fisheries in Madeira island and from a seizure of illegal fishing in the Selvagens islands, respectively. Each individual was measured (±1cm) and weighted (±1g) upon capture. White muscle was collected for measurement of mercury concentration.

Mercury concentrations were analysed using blood for the tuna species and muscle for the two other predators. By using the tuna's blood, we attempted to minimize the contribution of assimilated diet that would have been obtained in more distant waters used by tunas before arriving in Madeira. As it was not possible to collect blood for the two other predator species, white muscle was used instead. These predators are not known to perform long migrations like tunas (McClellan and Cummings 1997; Fontes and Afonso 2017), therefore, both tissues should represent the mercury values accumulated in the marine environment around the archipelago of Madeira. Because mercury accumulates differently among tissues (Storelli et al. 2005; Voegborlo et al. 2007), we also measured the concentration of mercury in the muscle of the same individuals of Bigeye tuna (n=20) that we analysed for blood (Supplementary Material, Figure A.1).

The blood and muscle tissues were first lyophilized and reduced into a homogenous powder that was then used to determine the total concentration of mercury. Samples (weighing 3-17mg) were analysed using thermal decomposition atomic absorption spectrometry alongside gold amalgamation in LECO AMA-254 equipment. A maximum coefficient of variation of 10% was defined for a minimum of 2 mercury readings (Furtado et al. 2019). Tort-2 and Tort-3 were used as the certified reference material to support the precision of the method (muscle tissue, certified value of

0.27±0.06 mg·kg^{-1} and 0.292±0.22 mg·kg^{-1}, respectively). The recovery efficiency for Tort 2 was 82.2±0.8% (n=6), and for Tort 3 was 84.4±2.4% (n=8). Mercury concentrations are reported on a dry weight basis (dw).

All statistical analyses were performed using R version 4.0.2 (R Core Team 2020).

Results

Bigeye tuna diet

A total of 762 prey items were found in 69 stomachs of Bigeye tuna (2 stomachs were empty), of which 95% were identified to family, genus or species level, resulting in 24 species, 23 genus and 20 different families. Fish was the most consumed prey, followed by cephalopods (Table 1). The Bigeye tuna presented an epipelagic diet (NF=84%) with only 9% of the prey (comprising the genus *Hygophum* and *Diaphus*) belonging to mesopelagic layers. The Atlantic chub mackerel *Scomber colias* was the most consumed species overall (NF=41%), followed by mackerel *Trachurus* sp. (NF=25%) and Longspine snipefish (NF=10%). Cephalopods comprised ca. 3.5% of the prey items. Other cephalopods, represented by older beaks with no remaining flesh, were also found in the stomachs of this tuna species (Supplementary Material, Table A.2). The Shannon-Wiener diversity for the Bigeye tuna was 1.79±0.14 (n=69).

The importance of the main prey of the Bigeye tuna changed between 2016 and 2017, with the number of Atlantic chub mackerel decreasing from 2016 to 2017 (NF=47% (n=642) to 2% (n=120)), and the number of Longspine snipefish increasing from 2% to 54% (NF) (Figure 2). However, Longspine snipefish were only found in 27% of the stomachs (n=11) in 2017 against the 12% of 2016 (n=58), while the Atlantic chub mackerel was found in 72% of the stomachs in 2016 and 45% in 2017. Finally, no variation in the consumption of mesopelagic and epipelagic were found between the different tuna length classes (PERMANOVA: $F_{2,65} = 1.03$, $r^2 = 0.03$, p=0.39).

Skipjack tuna diet

A total of 550 prey individuals were found in 57 stomachs of Skipjack tuna (4 empty stomachs), and 98% of the prey were identified resulting in 8 species, 10 genus and 8 families (Table 1). Fish was the most consumed prey by the Skipjack tuna, which also showed a preference for epipelagic species (NF=97%). The Longspine snipefish was the most consumed species (NF=35%), followed by Sand smelt *Atherina* sp. (NF=27%). The Atlantic chub mackerel and the European pilchard also had an important role in the

Skipjack tuna diet (NF=14% and 10%, respectively). The Shannon-Wiener Diversity Index for the Bigeye tuna was 1.59±0.12.

We found differences among years with the most consumed prey shifting from Sand smelt (NF=55%, n=138) and Atlantic chub mackerel (NF=33%, n=138) in 2016, to Longspine snipefish (NF=38%, n=292; FO=40%, n=30), European pilchard (NF= 19%, n=292) and Sand smelt (NF=16%, n=292) in 2017 (Figure 2). The consumption of Longspine snipefish increased even more in 2018 (NF=84%, n=120; FO=61%, n=13). No myctophids were found in Skipjack stomachs.

Table 1 - Diet of the Bigeye tuna *Thunnus obesus* and the Skipjack tuna *Katsuwonus pelamis* inferred through numeric frequency (NF) and frequency of occurrence (FO). Numbers between brackets represent the sample size

Taxa	**Family**	**Species**	**Bigeye**		**Skipjack**	
			NF (762)	**FO (69)**	**NF (550)**	**FO (57)**
Teleostei			**92.7**	**98.6**	**97.8**	**100**
	Scombridae	*Scomber colias*	41.1	69.6	14.4	47.4
	Carangidae	*Trachurus* sp.	25.7	69.6	4.5	21.1
	Centriscidae	*Macroramphosus scolopax*	10.6	14.5	35.8	35.0
	Atherinidae	*Atherina* sp.			27.1	36.8
	Sparidae	*Boops boops*	1.2	10.1	4.5	14.0
	Scomberesocidae	*Scomberesox saurus*	0.8	2.9		
	Clupeidae	*Sardina pilchardus*			10.4	22.8
		Sardinella sp.			0.2	1.8
		Unidentified			0.7	7.0
	Bramidae	*Brama brama*	0.3	2.9		
	Molidae	*Ranzania laevis*	0.3	1.4		
	Alepisauridae	*Alepisaurus ferox*	0.4	2.9		
	Paralepididae	*Arctozenus risso*	1.0	7.2		
		Sudis hyalina	0.1	1.4		
	Trichiuridae	Unidentified			0.2	1.8
	Nomeidae	*Cubiceps gracilis*	2.9	7.2		
	Scopelarchidae	*Scopelarchus* sp.	0.3	1.4		
	Myctophidae	*Diaphus sp.*	0.8	5.8		
		Diogenichthys atlanticus	0.1	1.4		
		Gonichtys cocco	0.1	1.4		
		Hygophum hygomii	0.1	1.4		
		Hygophum reinhardtii	0.3	1.4		
		Hygophum taaningi	0.4	1.4		
		Hygophum sp.	4.9	1.4		
	Unidentified fish		1.3	8.7		
Cephalopoda			**3.5**	**15.9**	**0.2**	**1.8**
	Mastigoteuthidae	*Mastigoteuthis* sp.	0.1	1.4		

	Ommastrephidae	*Todarodes sagittatus*	0.5	2.9		
		Ommastrephes bartramii			0.2	1.8
		Unidentified	0.5	5.8		
	Onychoteuthidae	*Onychoteuthis* sp.	0.5	2.9		
	Decapodiformes	*Unidentified*	0.3	2.9		
	Argonautidae	*Argonauta* sp.	0.3	2.9		
	Octopodidae	Unidentified	0.1	1.4		
	Unidentified cephalopod		1.2	4.3		
Arthropoda			**3.7**	**14.5**	**0.4**	**1.8**
	Penaeidae	*Funchalia villosa*	0.3	2.9		
	Decapoda	*Unidentified*	1.0	1.4		
	Platyscelidae	*Platyscelus* sp.	1.3	1.4		
	Unidentified crustacean		1.0	11.6	0.4	1.8
Gastropoda		Unidentified			**1.6**	**1.8**
Tunicata			**0.1**	**1.4**		
	Thaliacea	Unidentified	0.1	1.4		

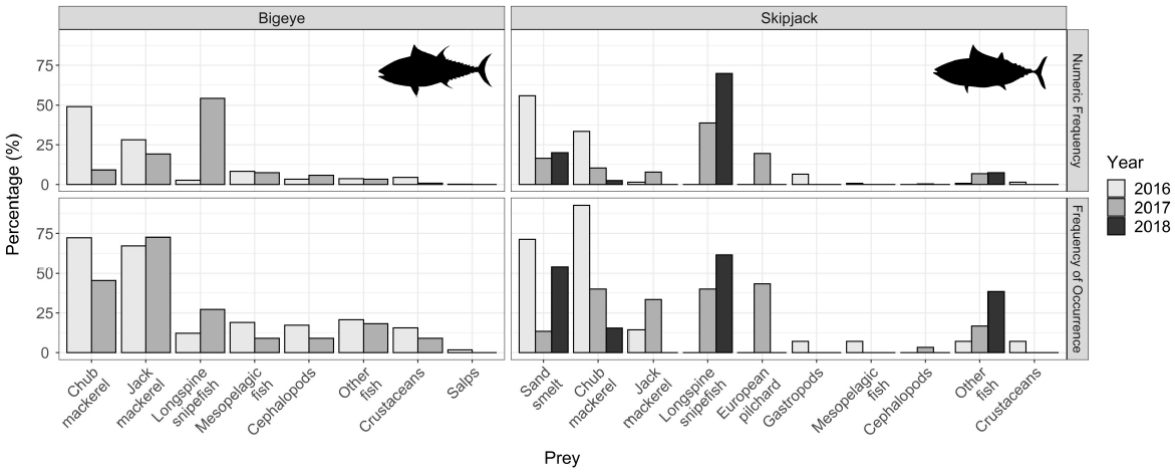

Figure 2 - Interannual variation of prey found in the stomachs of Bigeye *Thunnus obesus* and Skipjack tuna *Katsuwonus pelamis* captured in Madeira pelagic region in 2016-2018

Exclusion of bait from diet

Only trivial differences were found in the relative importance of prey in the diet of these tunas when all bait species with digestion levels I and II were excluded (Supplementary Material, section A1, Figure A.2 and A.3). Furthermore, in the stomach contents of Skipjack tunas captured in 2018 (when we had information on the bait used), we found highly digested remains (digestion state IV) of species used as bait and which should only be found undigested if the tunas only ate them as bait (Supplementary Material, section A.1, Table A.2).

Mercury concentration comparisons

Differences among predators in mercury concentrations were also found (ANOVA: $F_{3,82}$=22.35, p<0.001). Two distinct groups were observed: Bigeye tuna (blood) and Yellowmouth barracuda (muscle), which had the highest values, and Skipjack tuna (blood) and Longfin yellowtail (muscle) which presented the lowest values (Table 2). Only the Bigeye tuna presented a significant positive correlation between mercury concentration in blood and weight (r(18)=0.73, p=0.0002 on log transformed data) (Figure 3); individuals <100cm had 1.08±0.25 mg·kg^{-1} dw (0.57-1.58) and individuals >100cm had 2.12±0.96 mg·kg^{-1} dw (1.50-4.04).

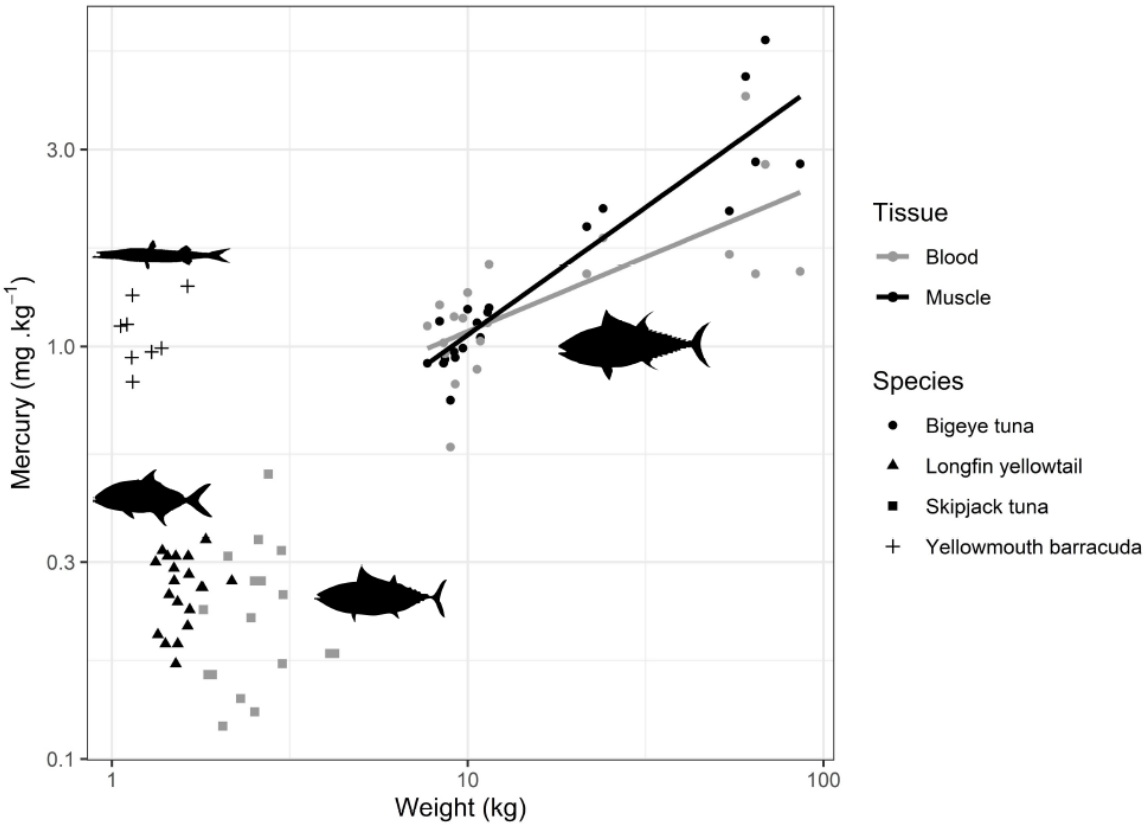

Figure 3 - Mercury concentration (mg·kg^{-1} dry weight) per fork length of each individual and species, Bigeye tuna *Thunnus obesus*, Skipjack tuna *Katsuwonus pelamis*, Yellowmouth barracuda *Sphyraena viridensis* and Longfin yellowtail *Seriola rivoliana*

Table 2 - Mercury concentrations (Hg; wet weight (ww); dry weight (dw) when mentioned) of tunas, yellowtails and barracudas worldwide. The wet-to-dry weight ratios were estimated as 1 $mg \cdot kg^{-1}$ wet weight to 3.3 $mg \cdot kg^{-1}$ dw (Houssard et al. 2019). Values are represented as Mean±SD (Min-Max), when possible

Species	Region	N	Tissue	Length (cm)	Weight (kg)	Hg ($mg \cdot kg^{-1}$)	Reference
Bigeye tuna *Thunnus obesus*	Madeira	20	Blood	97.6±35.8 (66-170)	25.2±25.6 (7.7-86.0)	1.44±0.76 **dw** (0.57-4.04)	This study
	Madeira	20	Muscle	97.6±35.8 (66-170)	25.2±25.6 (7.7-86.0)	1.76±1.29 **dw** (0.74-5.53)	This study
	Atlantic	30	Muscle	(60-167)		0.76 (0.34-1.29)	Besada et al. 2006
	NE Brazil	30	Muscle	(54-139)		0.545±0.339 (0.09-1.75)	Lacerda et al. 2017
	Azores	15	Muscle		10.6±0.8(SE)	0.14±0.08	Torres et al. 2016
	Atlantic	7	Muscle		38.9 (35-43)	0.27±0.01	Yamashita et al. 2005
	Atlantic	121	Muscle	(70-200)	56±33	0.89±0.47 (0.32-3.13)	Chen et al. 2011
	Pacific	30	Muscle		59.4 (41-99)	0.98±0.34	Yamashita et al. 2005
	Hawaii	50	Muscle	92±5 (84-98)		0.43±0.20 (0.15-1.01)	Ferriss and Essington 2011
	Taiwan	75	Muscle	140.8±27.4 (81-200)	53.4±28.1 (9-140)	0.93±0.67 (0.16-3.32)	Chen et al. 2014
	N Pacific	6	Muscle	113.7±33.5 (75-164)		0.54±0.21 (0.20-0.76)	Blum et al. 2013
	Hawaii	50	Muscle		41.2±20.4 (11.3-89.8)	0.6±0.3	Kaneko and Ralston 2007

	W Pacific	726	Muscle	91±31 (31-175)		0.43±0.48 (0.005-2.865)	Houssard et al. 2019
	Indian	27	Muscle	87±46		0.34±0.29	Bodin et al. 2017
	W Indian	110	Muscle	130±31 (53-198)	41±27 (1-110)	0.68±0.23 (0.22-1.88)	Chen et al. 2011
Skipjack tuna *Katsuwonus pelamis*	Madeira	18	Blood	49.9±3.4 (43-58)	2.6±0.7 (1.8-4.2)	0.23±0.09 **dw** (0.12-0.49)	This study
	Azores	53	Muscle	49.7 (28-84)		0.19 (0.09-0.34)	Andersen and Depledge 1997
	Azores	15	Muscle		3.3±0.2(SE)	0.04±0.01	Torres et al. 2016
	Canary Islands	132	Muscle			0.34 (0.15, min)	Armas et al. 1993
	Central N Pacific	10	Muscle		8.6±1.3 (6.4-10.4)	0.3±0.1	Kaneko and Ralston 2007
	N Pacific	6	Muscle	65.7±16.03 (35-80)		0.28±0.13 (0.06-0.41)	Blum et al. 2013
	Reunion Island	37	Muscle	68 (41-85)	9 (1-16)	0.67±0.26 **dw**	Kojadinovic et al. 2007
	W Indian	13	Muscle	57±10		0.21±0.11	Bodin et al. 2017
Longfin yellowtail *Seriola rivoliana*	Madeira	20	Muscle	43.8±1.6 (41-48)	1.6±0.2 (1.3-2.2)	0.26±0.05 **dw** (0.17-0.34)	This study
	Florida	17	Muscle	74.3 (43.8-84.0)		0.56 (0.1-1.4)	Adams et al. 2003
Seriola rivoliana + *Seriola dumerili*	Bermuda	17	Muscle		(ca. 0.6-4.7)	0.17±0.14 (0.03-0.53)	Dewailly et al. 2008
	Hawaii	8	Muscle	77.9±2.9		0.76±0.07 (0.51-1.12)	Sackett et al. 2015

Seriola dorsalis	California	72	Muscle	84.2±16.6 (50.7-120.7)		1.27±0.89 **dw**	Madigan et al. 2018
Yellowmouth barracuda *Sphyraena viridensis*	Madeira	8	Muscle	63±2.7 (59-67)	1.2±0.2 (1.1-1.6)	1.09±0.20 **dw** (0.82-1.4)	This study
Sphyraena barracuda	Florida	13	Muscle	109.5±12.98		1.71±0.88 (3.4, max)	Rumbold et al. 2018
	Florida	62	Muscle	62.8 (11.9-109.6)		0.87 (0.08-3.10)	Adams et al. 2003
Sphyraena sphyraena	Mediterranean	5	Muscle	(24.9-31.0)	(55.6-107.3)	0.21±0.12 (0.15-0.42)	Hornung et al. 1980

Discussion

The use of stomach contents allowed us to document the diet of the two most fished tuna species, the Bigeye and the Skipjack tuna, in the waters around the archipelago of Madeira. Here, both species presented a diet based on epipelagic organisms, and in the case of the Bigeye tuna complemented by some mesopelagic prey.

Diet of the Bigeye and Skipjack tuna

The diet of the Bigeye tuna captured in the archipelago of Madeira consists mostly of epipelagic fish prey, in contrast with what was found in other regions in the Atlantic and Pacific. The published evidence suggests that in both oceans, its diet consists mainly of mesopelagic species, both fish and cephalopods, such as Bramidae, Alepisauridae, Myctophidae, Gempylidae, Paralepididae (eg. Matthews et al. 1977; Moteki et al. 2001; Allain 2005; Young et al. 2010; Junior et al. 2012) and Ommastrephidae (Logan et al. 2013). These families were very scarcely represented, or entirely absent in our study. Besides our study, where Scombridae and Carangidae were the main prey items, only one other study performed in the equatorial eastern Pacific in a pole-and-line fishery, found the Bigeye tuna to mostly prey on an epipelagic species (the Buccaneer anchovy *Stolephorus buccaneeri*) (Hida 1973). In this region, the bait consisted mostly of 4 epipelagic forage fish which were unimportant as prey items (Hida 1973).

Bigeye tunas are known to perform daily vertical migrations, descending on average up to 500m during the day and ascending to the surface at night, to forage (Matsumoto et al. 2005). However, a study carried out in the Azores showed that the Bigeye tunas in this archipelago do not perform vertical migrations as deep as elsewhere (Arrizabalaga et al. 2008). In that region, tunas remained mostly in the upper 50m layer, rarely venturing beyond the 300m depth. Arrizabalaga et al. (2008) hypothesized that oceanographic features in the Azores would enhance primary production and concentrate tuna food resources in surface layers, allowing Bigeye tuna to forage on shallower waters. This may suggest that, like in Madeira, this tuna concentrates on epipelagic prey in the Azores. Alternatively, it could be that in the Azores mesopelagic prey are more accessible at shallow depths, which is strongly suggested by their prominence in the diet of surface foragers (Monteiro et al. 1996; Granadeiro et al. 2002). To our knowledge, there are no diet studies of Bigeye tuna performed in the Azores which could confirm or contradict any of these hypotheses.

Some studies have suggested that there is an ontogenetic variation in the diet of several species of tunas (eg. Graham et al. 2007; Lacerda et al. 2017), including the Bigeye tuna which feeds on a higher proportion of mesopelagic species when larger due to its higher capacity to reach greater depths (Ohshimo et al. 2018). However, in our study, we could find no differences in the diet of smaller and larger size-classes.

The diet of the Skipjack tuna in the archipelago of Madeira is similar to what has been documented in other regions of the Atlantic, with a predominance of Clupeidae, Scombridae, Carangidae and Serranidae (Postel 1955; Batts 1972; Dragovich 1970; Dragovich and Potthoff 1972). Around the Canary Islands, where pole-and-line technique with live bait (sardine and sand smelt) is also used, the diet of this species is composed mainly of Atlantic chub mackerel (Ramos et al. 1995). In the Pacific, families like Exocoetidae, Engraulidae and reef fish are also part of the skipjack's diet (Alverson 1963; Hida 1973; Allain 2005). In smaller proportions, mesopelagic species, such as Gonostomatidae, Gempylidae and Myctophidae are also part of its diet in the Atlantic and the Pacific oceans (Ahlstrom and Counts 1958; Dragovich 1970; Ankenbrandt 1985). Still, its diet is mostly epipelagic. In our study the only mesopelagic prey found was a Trichiuridae. Crustaceans, such as euphausiids (Ankenbrandt 1985), stomatopods and megalopa larvae, completed the diet of this tuna in several regions of the Atlantic and Pacific (Alverson 1963; Dragovich 1970; Batts 1972; Dragovich and Potthoff 1972; Bernard et al. 1985). However, in Madeira, the contribution of crustaceans was negligible.

As opportunistic species, tunas are known to shift their diet among foraging regions but also when prey community shifts (Olson et al. 2014). The increase of Longspine snipefish in the diet of the Bigeye and Skipjack tuna follows the trend already observed in the diet of the Cory's shearwaters *Calonectris borealis* in the same oceanic region (J. Romero unpubl. data), where the authors suggested that a shift happened in the pelagic community of the subtropical northeast Atlantic with an increase of the Longspine snipefish population from 2016 to 2017/2018.

The importance of bait in the diet of tunas

In this study, the characterization of the diet of the Bigeye and the Skipjack tunas considered the issues posed by the use of bait during the fishing events. The two predators which were used for comparison, the Yellowmouth barracuda and the Longfin yellowtail, feed on a

variety of schooling epipelagic species, such as engraulids, clupeids, scombrids, carangids and sparids (Allam et al. 1999; Barreiros et al. 2002, 2003; Kalogirou et al. 2012; Manooch and Haimovici 1983). It is worth mentioning that in the Azores, the main diet of barracudas and yellowtails are Blue jack mackerel and Atlantic chub mackerel (Barreiros et al. 2002, 2003). In the archipelago of Madeira, the yellowfin feeds on European pilchards and Blue jack mackerels (Cavaleiro et al. 2018) while the barracuda feeds on Atlantic chub mackerels (M. Hermida unpubl. data). These species corresponded to the main tuna prey we observed in this study.

The exclusion of the least digested prey used as bait in Madeira (see eg. Ankenbrandt 1985; Ramos et al. 1995) had minimal impact in the assessment of the diet. Furthermore, highly digested remains of bait species were found in Skipjack tunas, strongly suggesting they are also caught as natural prey. Therefore, the decision to exclude bait species from the diet analysis (rather than discarding only freshly ingested prey) as done in some studies (eg. Ankenbrandt 1985; Ramos et al. 1995), may be excluding prey that are actually important in the diet of these predators.

The analysis of mercury revealed two different groups of predators, one with higher concentrations (Bigeye tuna and Yellowmouth barracuda) and one with lower concentrations (Skipjack tuna and the Longfin yellowtail). Bigeye tuna showed slightly higher Hg values than the other predators, most likely because the diet of the former includes mesopelagic species, which have high concentrations of mercury (e.g. Monteiro et al. 1996). This is further supported by Choy et al. (2009) which concluded that predators with a mesopelagic diet have higher concentrations of mercury than those with an epipelagic diet. The barracuda also presented higher mercury values despite reportedly having an epipelagic diet. The reasons for this are still unknown, but the fact that Hg levels in Bigeye tuna are only slightly higher than in barracuda further supports the conclusion that mesopelagics are not an important component of the tuna's diet, or else we would expect a larger difference between these species.

Overall, the mercury concentrations in tissues of predators presented in this study are lower than in others from the Atlantic, Pacific, and Indian oceans (Table 2). While intraspecific differences in mercury burdens have also been attributed to the availability of mercury in different foraging regions (Peterson et al. 1973; Ferriss and Essington 2011;

Houssard et al. 2019), the use of conventional diet in our study, indicates that the differences in relation to other areas might be better explained by an epipelagic diet of the Bigeye tuna. Other variables, such as elimination and uptake rate of mercury, may explain the variations observed among species (Peterson et al. 1973). According to Ferriss and Essington (2014), the Skipjack tuna has a higher elimination rate than the Bigeye tuna (0.376 and 0.077 y^{-1}, respectively) which might explain the lower concentrations. Trudel and Rasmussen (1997) stated that the elimination rate responds negatively to the predator's body mass which could explain the differences between these two species. There are no elimination rates described for barracudas and yellowtails, remaining unclear what are the mechanisms driving the differences in mercury concentrations for barracudas and yellowtails.

The mercury values described in this study for the Bigeye, Skipjack, yellowtail and barracuda were obtained using blood for tunas and muscle tissue for the two other predators. When comparing the mercury values for blood and muscle for the Bigeye tuna, the calculated mean blood-muscle ratio was 1:1.17. This suggests that mercury levels in blood and muscle are broadly comparable, but more studies are needed to better assess that, as 3 (out of 20) of the individuals, which were also 3 of the biggest sampled tunas, presented higher mercury ratios.

The baseline information provided in this study raises new questions on the functioning of the ecosystem of this region. The Bigeye and the Skipjack tuna presented an epipelagic diet in the pelagic region of the archipelago of Madeira, which in the case of the Bigeye tuna suggests a different behaviour than the one often presented by this species. Further studies on the variability in oceanographic variables and its effects on the distribution and abundance of prey, as well as on the vertical movements of tuna in this area are required to understand their behaviour and explain why this mesopelagic predator presents an epipelagic diet in Madeira. The results of this study will allow for more informed decisions on an ecosystem-based fisheries management by considering not only the tuna but also the role they may have in the regional food webs and their interactions with other species.

Acknowledgements

This work was supported by Fundação para a Ciência e a Tecnologia (FCT Portugal) through the project Oceanwebs (PTDC/MAR-PRO/0929/2014) and Seamigrant (PTDC/BIA-ANM/3743/2014), the strategic projects UIDB/04292/2020 and

UIDP/04292/2020 granted to MARE, and UIDB/50017/2020 and UIDP/50017/2020 granted to CESAM. PD/BD/127810/2016 was granted to JR by FCT. MH was supported by a postdoctoral grant from ARDITI (Regional Agency for the Development of Research, Technology and Innovation of Madeira), Project M1420-09-5369-FSE-000001. BC was supported by a research grant within the project OceanWebs (PTDC/MAR-PRO/0929/2014). Bigeye tuna and barracudas used in this study were acquired by ARDITI through the Oceanic Observatory of Madeira Project (M1420-01-0145-FEDER-000001-Observatório Oceânico da Madeira-OOM). Skipjack tuna were acquired by the Regional Directorate of Fisheries (DRP) of Madeira, under the framework of the Programa Nacional de Recolha de Dados da Pesca (multiannual Union programme for the collection, management and use of data in the fisheries and aquaculture sectors). The authors are grateful to the Regional Directorate of Fisheries (DRP) of Madeira for their collaboration and support, particularly the Research Service director, João Delgado. Thanks are also due to Filipe Moniz and Carolina Vieira for helping sieving and identifying some of the stomach contents, and Cheila Raposo and Carolina Vieira for performing the mercury analysis.

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Supplementary Material

Table A.1 - Classification of the digestion level of tuna's prey for fishes and cephalopods according to Aloncle and Delaporte (1974) and Alonso et al. (2018), respectively.

Type of prey	Digestion Level	Description
Fish	I	The fish that was just swallowed, still presents all scales and original colour.
	II	The fish is whole but partly or entirely stripped of its scales and skin. Muscles are visible.
	III	The fish is split but the flesh is still attached to the skeleton.
	IV	The fish is only represented by skeleton debris.
Cephalopods	I	Cephalopod complete
	II	Mantle complete
	III	More than half of mantle present
	IV	Only a piece of mantle or isolated tentacles present
	V	Loose fresh beak (with flesh attached and/or not eroded)

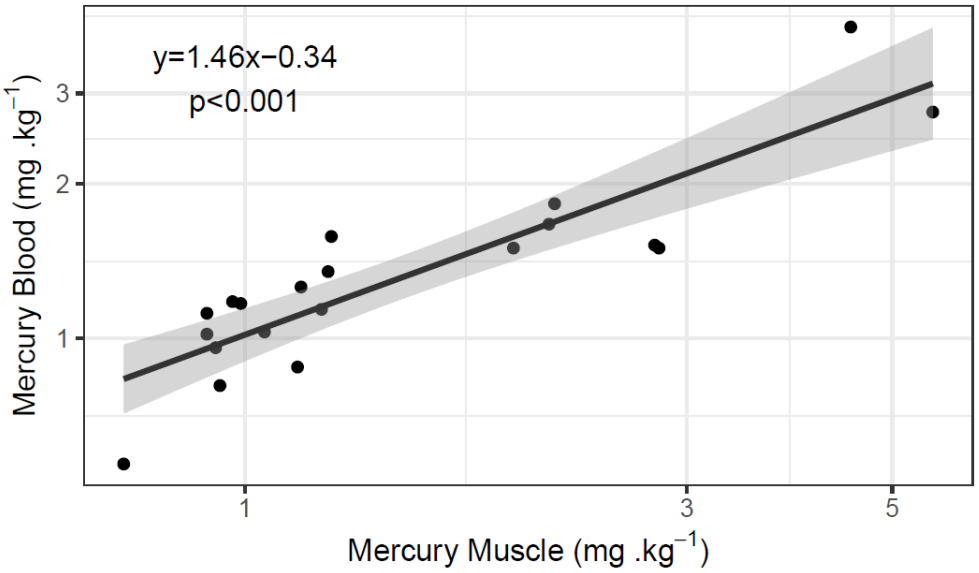

Figure A.1 - Regression between mercury concentration (mg·kg^{-1} dw) in blood and muscle of Bigeye tunas *Thunnus obesus* captured in the pelagic waters of the archipelago of Madeira.

Table A.2 - Cephalopod species present in the stomach contents of the Bigeye tuna *Thunnus obesus* and identified using their beaks. These beaks did not have any flesh attached which means that they were not ingested recently, and, therefore, were excluded from the diet characterization to avoid overestimation. NF – numeric frequency (sample size); FO – Frequency of occurrence (sample size).

Prey	**Order/Family**	**Species**	**NF (140)**	**FO (29)**
Decapodiformes				
	Mastigoteuthidae	*Mastigoteuthis* sp.	0.7	3.4
	Ommastrephidae	*Todarodes sagittatus*	4.3	10.3
		Unidentified	11.4	20.7
	Onychoteuthidae	*Onychoteuthis* sp.	10.0	10.3
	Brachioteuthidae	*Brachioteuthis riseii*	1.4	6.9
	Chiroteuthidae	*Planctoteuthis danae*	8.6	10.3
	Oegopsida	Unidentified	8.6	13.8
	Unidentified		17.9	24.1
Octopodiformes				
	Octopodidae	Unidentified	2.9	6.9
	Amphitretidae	*Japetella diaphana*	1.4	3.4
	Argonautidae	*Argonauta* sp.	4.3	10.3
	Argonautoidae (Superfamily)	Unidentified	0.7	3.4
Unidentified			**27.9**	**44.8**

A.1 - Bait

Removing prey with low digestion levels (I and II) from the analysis increased the percentage of empty stomachs from 3% to 32% (n=71) for the Bigeye tuna, and from 6% to 11% (n=61) for the Skipjack tuna. Still, no large shifts in the relative importance of prey were observed in the diet of these tunas, whether bait was included or not in the analysis (Fig. S2 and S3).

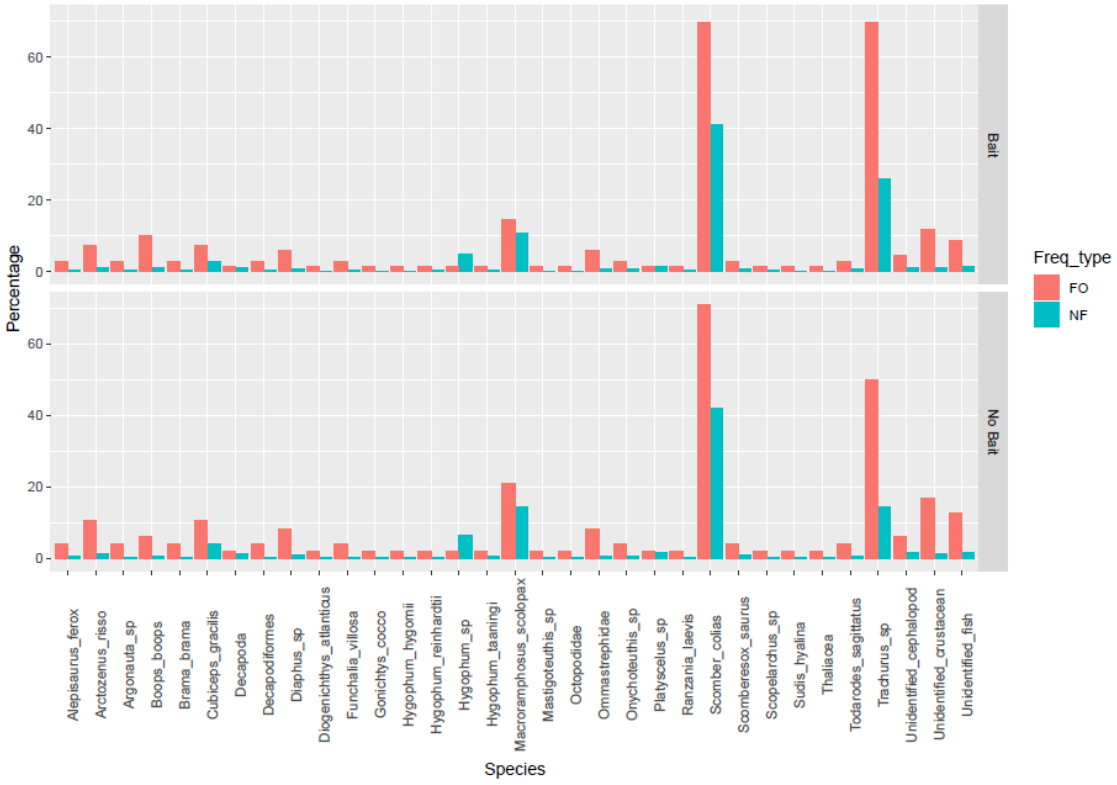

Figure A.2 - Diet of the Bigeye tuna *Thunnus obesus* (Numeric frequency - NF and Frequency of occurrence - FO) including all individuals found in the stomachs (n=69, Bait) and excluding bait species (Atlantic chub mackerel *Scomber colias*, mackerel *Trachurus sp.* and Bogue *Boops boops*) with digestion levels I and II (n=48, No bait).

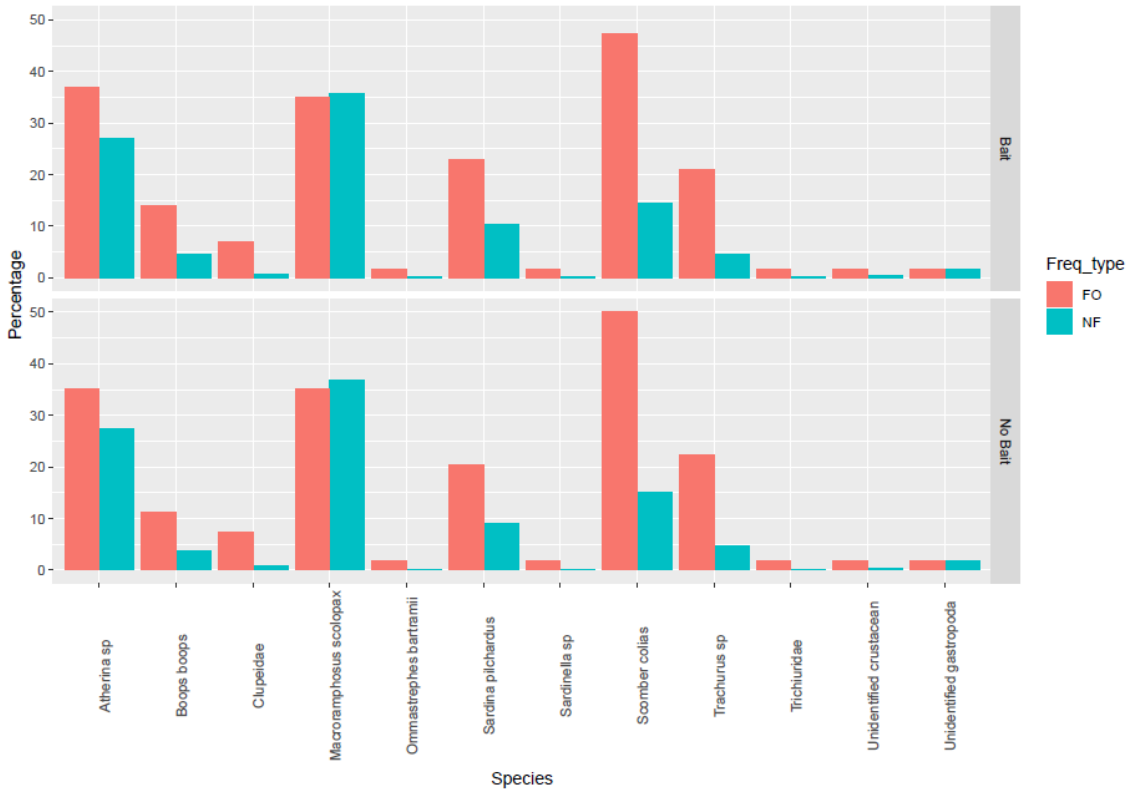

Figure A.3 - Diet of the Skipjack tuna *Katsuwonus pelamis* (Numeric frequency - NF and Frequency of occurrence - FO) including all individuals found in the stomachs (n=57, Bait) and excluding bait species (Sand smelt *Atherina sp.*, Bogue *Boops boops*, European pilchard *Sardina pilchardus*, and Longspine snipefish *Macroramphosus scolopax*) with digestion levels I and II (n=54, No Bait).

Table A.3 - Stomach contents of the Skipjack tuna Katsuwonus *pelamis* caught in Cardume in 2018 in the archipelago of Madeira and bait used in each fishing event

Bait	Stomach ID	Content	Number	Digestion level
Sardina pilchardus *Atherina* sp.	1	*Boops boops*	3	2-3
		Atherina sp.	1	4
	2	*Macroramphosus scolopax*	6	3-4
		Atherina sp.	1	4
	3	*Scomber colias*	2	3
		Macroramphosus scolopax	2	2-4
		Clupeidae	1	4
		Atherina sp.	2	4
	4	*Atherina sp.*	3	2
		Macroramphosus scolopax	24	3-4
	5	*Macroramphosus scolopax*	11	3-4
	6	*Atherina* sp.	5	2-4
		Macroramphosus scolopax	7	3-4
	7	*Atherina* sp.	8	2-4
		Macroramphosus scolopax	18	3-4
	8	*Atherina* sp.	4	2-3
		Macroramphosus scolopax	14	3-4
Sardina pilchardus *Boops boops* *Atherina* sp.	9	*Macroramphosus scolopax*	2	4
	10	*Boops boops*	3	1
	11	*Boops boops*	1	4
	12	*Boops boops*	1	4
	13	*Scomber colias*	1	4

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CHAPTER 4

Credits: Joana Romero

This chapter is published as:

Joana Romero, Paulo Catry, Dília Menezes, Nádia Coelho, João Paulo Silva, José Pedro Granadeiro (2019) A gull that scarcely ventures on the ocean: Yellow-legged gulls Larus michahellis atlantis on the oceanic island of Madeira. Ardeola 66: 101-112.

A gull that scarcely ventures on the ocean: Yellow-legged Gulls Larus michahellis atlantis on the oceanic island of Madeira

Abstract

The Yellow-legged Gull *Larus michahellis atlantis* (YLG) is a generalist and opportunistic species that explores different habitats and resources and easily adapts to humanised environments, sometimes posing problems related to aircraft security, public health or predation on other species, for example. We examined the distribution and foraging behaviour of YLGs on the oceanic island of Madeira. GPS-GSM devices were deployed on ten breeding individuals and samples of blood (adults) and feathers (chicks) were collected to examine their stable isotope signatures in relation to those of their prey. Tracked YLGs did not migrate. Birds remained mostly inland during the day (up to 60% of fixes) and barely 5% of the fixes were at sea. Eighty-eight out of 192 gull trips to the sea were in interaction with local fishing vessels, 91% of which involving purse seiners that were active at night. The diet of the adult YLGs consisted of refuse, fish and small petrels, whereas the chick diet included mainly fish. YLGs on this oceanic island are strongly dependent on anthropogenic resources, scarcely relying on natural marine prey. The desired control of this gull population could perhaps be achieved by the reduction of accessibility to organic waste.

Keywords: Fishing activity, GPS tracking, Habitat-use, Human waste, Stable isotopes

Introduction

Populations of large gulls, including Yellow-legged Gulls *Larus michahellis atlantis* (YLG) have been increasing continuously over the past century (eg. Harris, 1970; Duhem *et al*., 2008). Their generalist and opportunistic behaviour allows them to exploit different environments and resources within both natural and human-modified areas (Moreno *et al*., 2010; Navarro *et al*., 2017). Overall, YLGs can be found in both terrestrial and marine environments, the later mostly used to forage (Arizaga *et al.,* 2010; Ceia *et al.,* 2014), often in association with human activities (*e.g.* at harbours, fishing vessels). Their marine-based diet comes to some extent from natural prey but in many areas is primarily obtained from fishing discards (Oro *et al.,* 1995; Ceia *et al.,* 2014). Interactions between gulls and fishing vessels are a well-known and widespread phenomenon, mainly involving trawlers due to their high discard rates (Camphuysen *et al.,* 1993; Garthe *et al.,* 1996; Karris *et al*., 2018). Refuse dumps are also important reliable locations for gulls to obtain food (Duhem *et al.*, 2003; Arizaga *et al.,* 2014; Navarro *et al.,* 2016). The plastic behaviour showed by YLGs has led to overpopulation in many areas, which has turned this species into an important safety and public health hazard (Ramos *et al.*, 2009b; Ramos *et al.*, 2010). Its predatory behaviour also poses challenges to the conservation of rarer species (Hernández-Matías & Ruiz, 2003; Matias & Catry, 2010).

YLG populations at mainland coasts and estuaries are well studied but there is comparatively little information regarding their distribution and behaviour on oceanic islands, other than some dietary information (eg. Matias & Catry, 2010; Pedro *et al.,* 2013; López *et al.,* 2016). We examined the foraging behaviour and distribution of YLGs breeding on the Portuguese archipelago of Madeira, a group of oceanic Atlantic islands surrounded by oligotrophic waters. In particular, we aimed to investigate the distribution, habitat-use and daily activity patterns of YLGs, to quantify the relationship between gulls and fishing vessels and to assess the importance of natural prey in their diet. There is no trawler fleet in Madeira (Vallerani *et al.*, 2017), which leads us to hypothesise that the Madeiran YLG population is less dependent on marine resources despite inhabiting an environment surrounded by sea.

Methods

Study area

The YLG has three main breeding colonies on Madeira island (32˚40’08.97’’ N, 16˚55’28.06’’ W), on the uninhabited islets of Desembarcadouro and Chão and on small islets close to Porto Santo island. This work was carried out on Desembarcadouro islet (46ha), which is almost contiguous with Madeira, and on Chão islet (43ha), *c.* 20km SE of Madeira. The breeding populations of Desembarcadouro and Chão islets have been estimated at about 1,900 and 600 breeding pairs, respectively.

GPS-tracking and gull distribution

In late April 2016 and 2017, six GPS-GSM devices were deployed on incubating birds on Chão islet, and three on Desembarcadouro islet, respectively. A tenth device was deployed only in late May 2017, on Desembarcadouro islet. All birds were marked with a metal ring, weighed and had devices deployed on their backs with a wing teflon harness (Thaxter *et al.,* 2014). The sex of the birds was unknown. The GPS-GSM devices were solar powered and measured 57x26x20mm and weighed 27g (Movetech Telemetry, maximum error ca. 100m), corresponding to *c*. 3% of the bird weight (870±106g, n=15 birds), and recorded fixes every 30 minutes under a normal regime and every two minutes if the battery level was very high. In parallel, we carried out point-counts in January 2017 at strategic sites, to assess the distribution of the YLG around the entire island of Madeira (Supplementary material appendix 1, A1). All procedures were approved by the Animal Welfare Body of the University of Lisbon (2/2016, 8th March 2016) and by National Authorities (0.421/2016, 14th November 2016).

The distribution of birds in the study area was described using a kernel density map on projected coordinates, using the *adehabitatHR* package (h=0.018, grid=300; Calenge, 2017), under R software (R Core Team, version 1.0.143) (Supplementary material appendix 1, A2).

Assessing gull activity in relation to fisheries

We characterised the activity area of the local fishing fleet using data from the Terrestrial Automatic Identification System (AIS-T, obtained from www.marinetraffic.com) complemented by data from the Vessel Monitoring System (VMS) collected for the study area (provided by the DGRM, see acknowledgements), covering April to September 2016

(Supplementary material appendix 1, A2). This period coincided with the highest number of gulls with at-sea positions.

To quantify the relative utilisation of used areas, four different habitat categories were defined: land (golf fields, urban solid waste treatment plant, wind farm fields, open fields), harbours (at Funchal and Caniçal), coastline (inland and sea area within 500m from the coastline, excluding harbours), and offshore (beyond 500m offshore l). The usage intensity of each habitat category was calculated as the mean proportion of positions in each one at each hour of the day by the study birds, as obtained by the GPS loggers (Supplementary material appendix 1, A2). Fixes were filtered to exclude all positions taken at intervals shorter than one hour. Hence, to estimate the time spent in each habitat category, we considered that each fix corresponded to one hour.

We produced a time-synchronised animation of non-filtered data of gulls and fishing vessels during the previously referred period to investigate the occurrence of gull-fishing vessel interactions (Granadeiro *et al*., 2011) (Supplementary material appendix 2, Video B4). To describe this behaviour, we recorded the number of gull trips, the number of fishing vessel trips, the number of gull-vessel interactions and the time. For the analysis of the interactions with fishing vessels, we defined a trip as a set of consecutive positions at sea, i.e. farther than 500m from the coast, between two positions on land. An interaction was considered to exist when one gull headed directly towards a fishing vessel and its position was within a 500m radius of the fishing vessel. Gull trips were considered to occur in daylight or in darkness according to the time of local sunrise and sunset (below the horizon) calculated for each day.

Diet assessment

In late April 2016, we collected blood for stable isotope analysis (SIA) from 15 individuals. Additionally, in late May 2017, we collected 20 regurgitations and 15 samples of growing body feathers from chicks from different broods at Desembarcadouro islet. We calculated frequencies of occurrence as the percentage of regurgitated samples with a given prey type, and numeric frequencies as the number of individuals of each prey type in relation to the total number of individuals. Muscle samples were collected from the regurgitations. Other prey for SIA (known from the literature or personal observations to figure in the YLG diet), including snails, rabbits, Bulwer's Petrels *Bulweria bulwerii* and cow meat were

opportunistically collected (Jorge Camacho *et al.*, 2000; Matias & Catry, 2010; Alonso *et al.*, 2015) (Supplementary material appendix 1, A3).

SIA was carried out using continuous-flow isotope-ratio mass spectrometry (CF-IRMS) (Brand *et al.*, 2015). The contribution of different food sources to the diet of YLGs in Madeira was described using mixing models as implemented in the SIAR package for R (Parnell *et al.*, 2010) (Supplementary material appendix 1, A3).

Results

Distribution of the Yellow-legged Gull

The deployment of the ten GPS-GSM devices, resulted in an average of 1132.6±1107.4 hourly fixes per individual (range: 13 to 306 days), from 27th April 2016 to 23rd December 2017.

YLG fixes were concentrated in the south-eastern part of Madeira island. The 50% density contour showed a narrow area of occupancy including the city of Funchal, the Urban Solid Waste Treatment Plant (USWTP) and Santo da Serra golf field (Figure 1). The point-counts conducted on Madeira island (Supplementary material appendix 2, Figure B1) mostly suggested a similar distribution pattern during winter, except for some concentrations in the north-west of the island. A total of 1,662 YLGs were found during these counts.

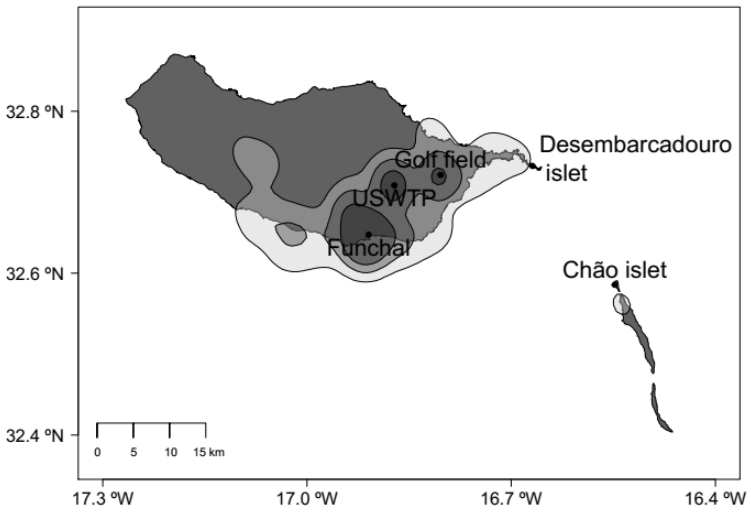

Figure 1 - Distribution of Yellow-legged Gulls *Larus michahellis atlantis* on Madeira island from 27th April 2016 to 23rd December 2017. Kernel density contours correspond to 95%

(lighter shade), 75% and 50% (darker shade). USWTP - Urban Solid Waste Treatment Plant. Desembarcadouro and Chão islets are the study breeding colonies.

During the entire annual cycle, GPS-tracked gulls never left Madeira island and Chão islet, keeping within a radius of 56km from Desembarcadouro islet and 70km from Chão islet, and never venturing out into the ocean proper. Excluding commuting movements between Chão islet and Madeira, all positions recorded at sea were within 5km of the coastline, with 61% within 2km of the coastline. Of the GPS positions 94% were terrestrial or less than 2km offshore.

Gull activity in relation to fisheries

Most fixes (up to 60%) were obtained inland during the day but during the night they were mostly concentrated in the harbours and at-sea areas (Figure 2). Only 6% were at sea (i.e., farther than 500m from the coast), 70% of which were at night.

The fishing activity and the positions of gulls while at sea showed considerable overlap (Supplementary material appendix 2, Figure B2). The analysis of the animations of time-matched gulls and fishing vessels movements in that area, revealed that (at least) 46% of gull trips to the sea involved an interaction with a fishing boat (n=192 trips) and that 91% of those interactions were with three purse seiners. Most (94%) of the interactions (n=89 interactions) occurred between 22:00 and 03:00 (GMT) and purse seiner activity was concentrated between 16:00 and 06:00.

Diet

Most (80%) of the regurgitations from chicks included marine fish, mainly Blue Jack Mackerel *Trachurus picturatus* and Atlantic Chub Mackerel *Scomber colias* (Table 1). Unidentified fish consisted of pieces with no hard structures that allowed identification and eight small fish found in one regurgitation (Table 1). All food sources were well segregated in at least one of the isotopes ($\delta^{13}C$: ANOVA, $F_{3,26}=28.5$, $P<0.001$; $\delta^{15}N$: ANOVA, $F_{3,26}=30.2$, $P<0.001$) (Figure 3, Supplementary material appendix 2, Figure B3). The results of the mixing models revealed that refuse, marine fish and Bulwer's Petrels constituted the bulk of the diet of adult YLGs (Figure 4a), whereas chicks were mostly fed on fish (Figure 4b).

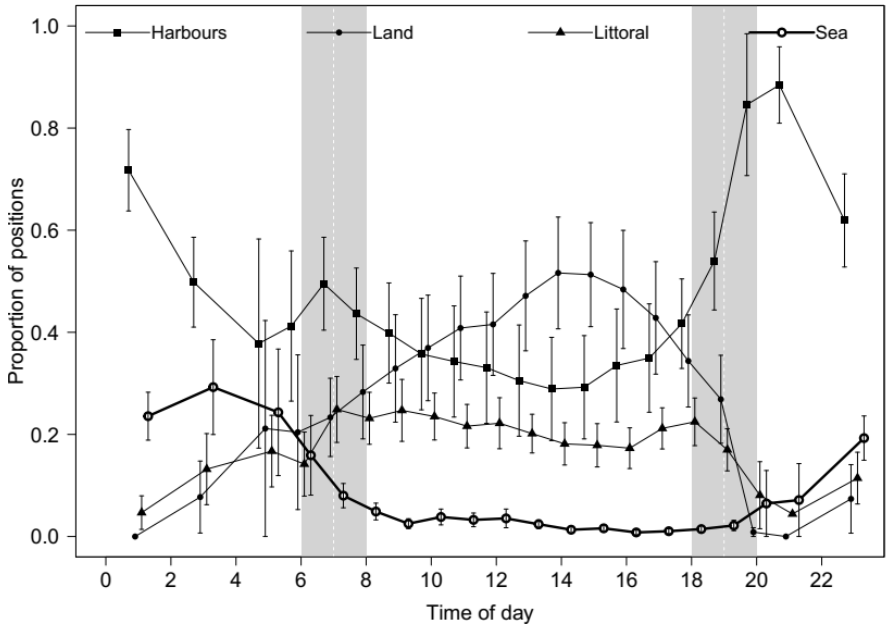

Figure 2 - Proportion of positions (±SE) of Yellow-legged Gulls *Larus michahellis atlantis* in each habitat category at each hour of the day during the study period, on Madeira island. The shaded areas represent the variation in the sunrise and sunset period throughout the year in Madeira. The sunrise/sunset calculation was done using a 0˚ inclination of the sun in relation to earth.

Table 1 – Diet of Yellow-legged Gull *Larus michahellis atlantis* chicks on Desembarcadouro islet, in May 2017 (n=20 regurgitations).

Food item	**Numeric Frequency (%) (n=29 prey items)**	**Frequency of Occurrence (%) (n=20 regurgitations)**
Fish Atlantic Chub Mackerel *Scomber colias*	13.8	30
Blue Jack Mackerel *Trachurus picturatus*	10.3	15
Common bogue *Boops boops*	3.5	5
Unidentified	44.8	30
Insects Wart-biter *Dectitus albifrons*	17.2	10
Refuse Chicken meat *Gallus domesticus*	3.5	5
Potato *Solanum tuberosum*	3.5	5
Pork meat *Sus domesticus*	3.5	5

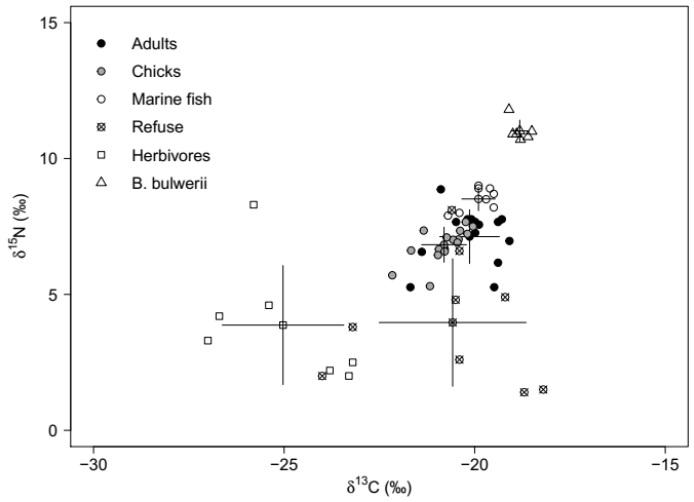

Figure 3 - Distribution of mean (±SD) δ13C and δ15N of adults (blood from April 2016, Chão islet) and chicks (feathers from May 2017, Desembarcadouro islet) of Yellow-legged Gulls *Larus michahellis atlantis* and food categories: Terrestrial herbivores (snails, wart-biters and rabbits), Marine fish (Blue Jack Mackerel, Atlantic Chub Mackerel and Common Bogue), Refuse (chicken, pork and cow meat), and Bulwer's Petrel. Adult and chick stable isotope values are represented after correction for trophic discrimination (i.e. after subtracting 0.38‰for $\delta^{13}C$ and 2.93‰for $\delta^{15}N$ for blood, and 1.97‰for $\delta^{13}C$ and 4.00‰for $\delta^{15}N$ for feathers).

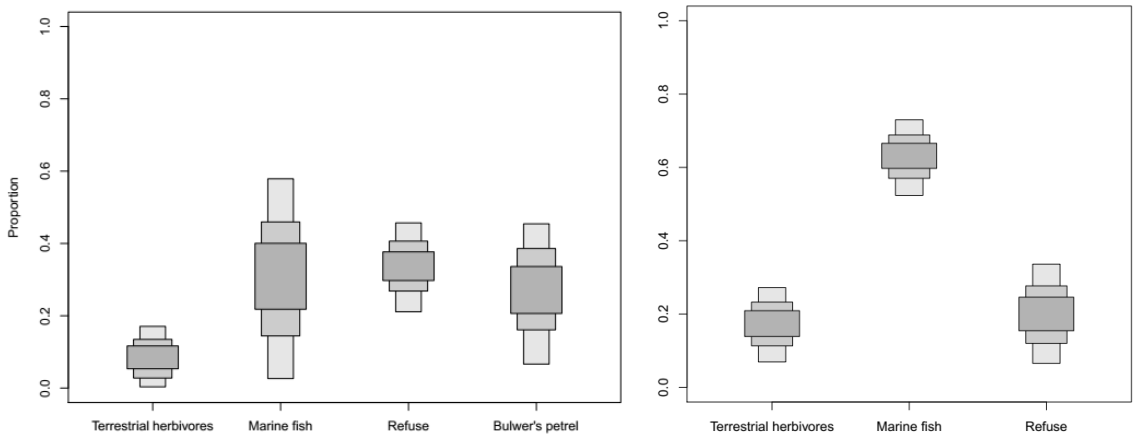

Figure 4 - Proportion of each food category ingested by (a) adults and (b) chicks of Yellow-legged Gull *Larus michahellis atlantis* in April 2016 in Chão islet, and May 2017 in Desembarcadouro islet, respectively. Terrestrial herbivores include snails, wart-biters and rabbits, Marine fish includes Blue Jack Mackerel, Atlantic Chub Mackerel and Common Bogue, Refuse includes chicken, pork and cow meat.

Discussion

This study investigated the distribution and diet of the YLG on the oceanic island of Madeira. Gulls used mainly human-modified terrestrial environments to feed and rest and made very little use of the marine environment and its natural resources. This limited at-sea activity was mainly associated with purse seiners, which operate near shore and at night. Adult diet included large proportions of refuse, marine fish (probably from fishery discards) and Bulwer's Petrels. The chick diet mainly consisted of marine fish.

Distribution of the Yellow-legged gull

Gulls generally used a relatively small part of Madeira island, mostly occupying human-modified locations, such as the urban solid waste treatment plant (USWTP), golf courses, reservoirs and harbours. Although this is common behaviour for this species, reported in other European populations (Navarro *et al.*, 2017), the YLG population of Madeira stands out for the rare use that it makes of marine environments, which are highly used by continental populations (Ramos *et al.*, 2009a; Ceia *et al.*, 2014). Although our sample size of tracked gulls was small (ten), the distribution obtained was likely to be representative of the population as it was well-matched by the results of the point-counts made around the island during winter, which found 1,662 gulls. The gull distribution and abundance are likely influenced by the greater human presence in the southeast of the island (DREM, 2017) and by greater food availability, mainly of anthropogenic sources, in that area.

Our data confirms that the Madeiran adult population of YLGs is resident. There were no movements farther than *c.* 70km from the breeding colony or farther than 5km from the coastline during the two years that the gulls were tracked.

Gull activity in relation to fisheries

During the day, the gulls mainly used inland areas, whereas at night they moved to harbours, probably to rest. Movements to the sea were occasional and 70% of those trips were between sunset and sunrise, which contrasts with other studies that have reported mostly diurnal activity at sea in synchronisation with fishing vessels present in those areas (González-Solís *et al.*, 1997, 1999). The vessel activity data used in our study was quite complete, including both AIS-T and VMS systems. These surveillance systems are not mandatory in small fishing boats, which were not detected, but such boats are also less likely to produce discards that might attract gulls. Most at-sea positions of gulls took place at night,

when purse seiners comprise the principal fishing gear operating (Vasconcelos *et al*., 2006). This fleet is active from late afternoon until morning, probably explaining the nocturnal at-sea activity by YLGs. The fishing fleet registered in Madeira constitutes 468 vessels, of which 395 are tuna fishing vessels, 58 use longlines for Black Scabbardfish fishing and three vessels use trolling lines for large pelagic fish. Traps and gillnets are used by five and two vessels, respectively. Purse seiners constitute only 1% of the fishing fleet with five vessels that mainly target Atlantic Chub Mackerel *Scomber colias* and Blue Jack Mackerel *Trachurus picturatus* (Hermida & Delgado, 2016; Vallerani *et al.*, 2017). Interactions with vessels other than purse seiners were scarce, most probably because they produce comparatively few discards or refuse and often operate away from the coast. The low at-sea activity of YLGs in Madeira likely reflects the small size of the purse seiner fleet and the absence of a trawling operation in the area (Camphuysen *et al.,* 1993; Garthe *et al.,* 1996).

Diet

The SIA revealed that adult YLGs consumed mostly refuse, followed by marine fish and Bulwer's Petrels. YLGs frequently prey on small petrels (Neves *et al*., 2006; Matias & Catry, 2010) and in the region of the studied gull colonies there is a very large aggregation (*c.* 45,000 pairs) of Bulwer's Petrels (Catry *et al*., 2014-15). Further, we have witnessed cases of predation on Bulwer's petrels by gulls in the study area. Nevertheless, the estimates of marine fish and Bulwer's Petrel provided by the SI mixing model were negatively correlated (Supplementary material appendix 2, Figure B3), which raises some uncertainty regarding the relative importance of Bulwer's Petrels on the diet of the YLG population from Madeira. Moreover, several other sources of information (e.g. pellet analysis and behavioural observations from unpublished author's information) suggest that the dietary contribution of Bulwer's Petrel may be overestimated by our model at the cost of marine fish, and this issue can only be resolved with more in-depth research. Nevertheless, we believe that the high contribution of refuse fits well with the frequent use of the urban solid waste treatment plant, and that the availability of fish provided by local purse seiners justifies the importance of marine fish, particularly during chick-rearing period. The low use of the marine environment by the gulls in our study and the frequent interactions with fishing vessels suggest that most of the fish consumed is of anthropogenic sources and mainly taken from purse seiners at night, rather than obtained as discards. A high consumption of food from terrestrial sources

by YLGs has also been described on other oceanic islands, namely in the Azores (Neves *et al.*, 2006; Pedro *et al.*, 2013), the Canary islands (Jorge Camacho *et al.*, 2000; López *et al.*, 2016), and on Selvagem Grande Island (Matias & Catry, 2010), where gulls consume mostly refuse, terrestrial invertebrates, seabirds (captured on land) and land snails, respectively. This somewhat contrasts with mainland Europe, where the diet of YLGs is mainly of marine origin, even though a considerable proportion of it probably originates from discards (González-Solís *et al.*, 1997; Ceia *et al.*, 2014; Alonso *et al.*, 2015; Calado *et al.*, 2018; Morera-Pujol *et al*., 2018). Nonetheless, there are also instances in the western and north-western Mediterranean where terrestrial food sources (refuse and terrestrial invertebrates) are the main food components (Duhem *et al.*, 2003).

In Madeira, YLG chicks were mostly fed marine fish. Adults do not seem to rely on marine resources, so it is likely that purse seiners play an important role in the reproductive success of this population. This seems to be typical for chicks of YLG from various populations (Arizaga *et al.*, 2010, 2013; Ramos *et al.*, 2009b), although variations and alternative prey have also been reported (Pedro *et al.*, 2013; Ceia *et al.*, 2014; Alonso *et al.*, 2015).

The findings of this study confirm that Madeiran YLGs do not exploit natural prey in the pelagic deep-sea environments, as found around the archipelago. This large population apparently thrives due to the existence of anthropogenic food subsidies, mostly obtained inland and also during interactions with purse seiners.

Acknowledgements

This work was supported by the European Commission through the LIFE project - LIFE RECOVER NATURA (LIFE12 NAT/PT/000195), and Fundação para a Ciência e a Tecnologia (FCT Portugal) through the project Oceanwebs (PTDC/MAR-PRO/0929/2014), the strategic projects UID/MAR/04292/2013 granted to MARE and UID/AMB/50017/2013 granted to CESAM (with co-funding by FEDER, within the PT2020 Partnership Agreement and Compete 2020), and the project IF/00502/2013/CP1186/CT0003 and PTDC/BIAANM/3743/2014. PD/BD/127810/2016 and SFRH/BPD/111084/2015were granted to JR and JPS, respectively, by FCT. We would like to acknowledge the Instituto das Florestas e Conservação da Natureza, especially Dr. Paulo Oliveira, for permission to undertake experiments with birds and logistical support to carry out the work on the islands

of Desertas and Madeira. Thanks are due to the Direcção Geral de Recursos Naturais, Segurança e Serviços Marítimos (DGRM) for providing the Vessel Monitoring System Data. We also thank the valuable help given by park-wardens Carlos Clemente, Manuel José, Isamberto Silva and volunteers, in the field, and Filipe Moniz, Mafalda Pádua, Gabriel Mendes and Rafael Luís for assistance with laboratory work. We thank to the anonymous reviewer and the editor for the helpful review of the manuscript.

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Supplementary Material 1

Supplementary material appendix 1, A1: Methods for point-counts of gulls in winter

We carried out 19 point-counts at strategic sites around the island of Madeira (14 points) and at five other locations further inland to assess the distribution of the Yellow-legged Gull *Larus michahellis atlantis* (YLG) on that island. Counting points were initially selected from a 1km grid all around the island, but some quadrats that were not easily accessed by car were not counted. This work took place during two days in January 2017 and involved counting (with a telescope 20x) all individuals visible, whether landed, flying or feeding, within 1,000m. No distinction was made between adults and immature birds.

Supplementary material appendix 1, A2: Filtering of the gull tracking data, and AIS-T and VMS data

We deployed GPS-GSM devices on ten YLGs in Madeira island with the aim of describing the distribution of the population. Some technical problems arose causing for larger intervals between positions taken, leading to the need of data regularisation. Hourly positions were more frequent and congruent throughout all GPS devices; therefore, we regularised all trajectories by linear interpolation of fixes. Also, different GPS units recorded data over different periods. Therefore, some of the analyses were based on randomly sampled fixes from each individual, based on the GPS with the smallest number of fixes (n=176). To study the areas used by the gulls in Madeira, both for foraging and resting, we excluded the fixes at colonies. At-sea positions between the breeding colony, Chão islet and the main island were completely linear and represented commuting movements between the islands, not foraging activity, so were also excluded. The previous conditions were applied to all tracking data analyses.

VMS and AIS-T data were used to characterise the activity area of fishing vessels in the vicinity of Madeira island at the time positions of YLGs were present in the sea. VMS data were preferably used while AIS-T data complemented the database with a few fishing vessels that were not present in the VMS dataset. The sampling intervals of VMS and AIS-T data differed among vessels and therefore we regularised the data by only keeping vessel positions that differed by at least one hour. Furthermore, we filtered these positions for speeds under 4 knots. The AIS-T and VMS data represented a total of 123 vessels and 10,854 vessel positions, and the analysed timespan included 6 gulls. We then constructed a 50%, 75% and

95% kernel density of fishing vessels in activity, using filtered AIS-T and VMS data and the *adehabitatHR* package (h=0.03, grid=300; Calenge, 2017), under R software (R Core Team, version 1.0.143).

Supplementary material appendix 1, A3: Stable Isotope Analysis and treatment of blood, feathers and muscle

To assess the diet of the YLGs in the Archipelago of Madeira, we used stable isotope analysis of adults (blood) and chicks (feathers) of YLGs and their preys (muscles), collected in April 2016 and May 2017. The feathers collected from chicks had just grown, which meant that the isotopic signature represented the diet consumed during the chick rearing period. Because feathers of adults start moulting later in August (Monteiro *et al*., 1996), after the chick rearing, they represented a different time period than that of the chick feathers. Therefore, blood of adults was collected for comparison of the same period as the chicks.

Spontaneous regurgitations of chicks provided some diet samples, and prey were identified to the lowest taxonomic level, using hard structures like vertebrae and/or otoliths, and an extensive reference collection. Among prey species identified were fish (*Scomber colias*, *Trachurus picturatus*, *Boops boops*), wart-biters (*Dectitus albifrons*), and pork and chicken meat.

Bulwer's Petrels have never been found in chick regurgitations or ever described as a dietary item, unlike in adults (Ramos *et al.*, 2009a, Arizaga *et al.*, 2010, 2013, Alonso *et al.*, 2015). Therefore, Bulwer's Petrels were not considered to represent prey in the chick diet.

Feathers were washed with 10% NaOH solution to clean them from external particles (Bearhop *et al.*, 2000, Arizaga *et al.*, 2013), and then thoroughly washed with distilled water. Blood samples from adults did not undergo any treatment before isotopic analysis (Bearhop *et al.*, 2000, Granadeiro *et al.*, 2013). Prior to isotopic analysis of Carbon and Nitrogen, muscle samples from prey were treated with a 2:1 chloroform-methanol solution to extract the lipids of the tissues.

SIA was carried out using continuous-flow isotope-ratio mass spectrometry (CF-IRMS) (Brand *et al.*, 2015). Results are represented in parts per thousand (‰) relative to the Pee Dee Belemnite (PDB) for $\delta^{13}C$, and atmospheric nitrogen for $\delta^{15}N$. The contribution of different food sources to the diet of YLG in Madeira was described using mixing models as

implemented in the SIAR package for R (Parnell *et al.*, 2010). Prey were grouped according to their trophic guild: terrestrial herbivores (including snails, wart-biters and rabbits), refuse (chicken, pork and cow meat), marine fish (Atlantic chub mackerels, blue jack mackerels and bogues), and Bulwer's Petrel. We could not find discrimination factors for diet-blood and diet-feather for YLG, and therefore we calculated average values derived from literature (Hobson & Clark, 1992, Mizutani *et al.*, 1992, Bearhop *et al.*, 1999, 2002, Ogden *et al.*, 2004, Cherel *et al.*, 2005, Williams *et al.*, 2007, Ramos *et al.*, 2009b): diet-blood: 2.93±0.45‰ for $\delta^{15}N$ and 0.39±0.96‰ for $\delta^{13}C$, and diet-feather: 4.00±1.07‰ for $\delta^{15}N$ and 1.97±1.54‰ for $\delta^{13}C$.

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Supplementary Material 2

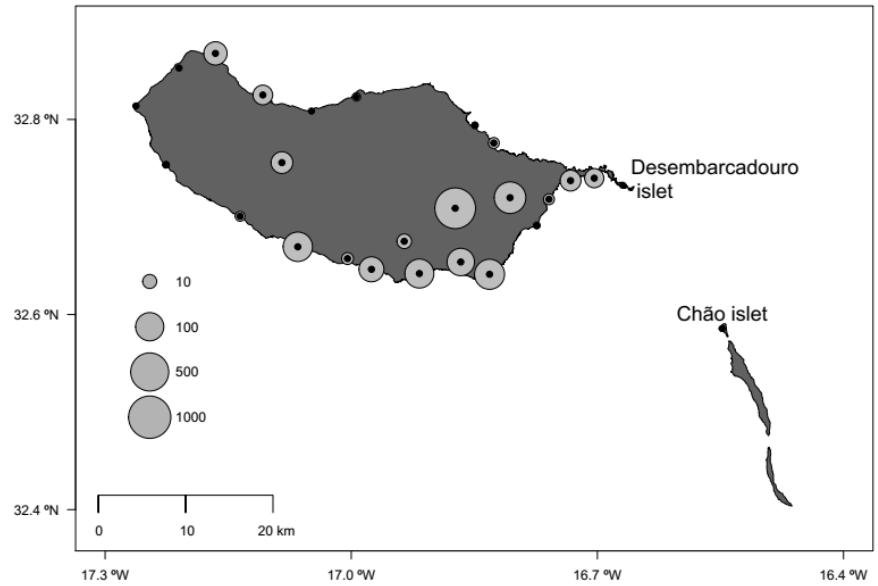

Figure B1 - Total numbers of Yellow-legged Gulls *Larus michahellis atlantis* at each point-count site (black points) in January 2017, in Madeira island. Desembarcadouro and Chão islet are the breeding colonies studied.

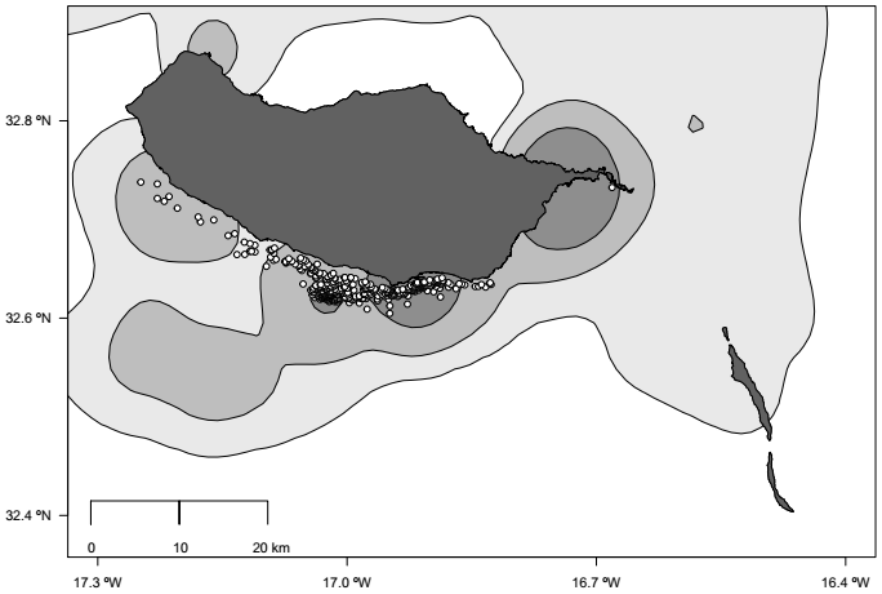

Figure B2 – Kernel density estimates of fishing activity (vessels travelling at <4 knots) around Madeira island, from 1st April 2016 to 30th September 2016 and at-sea positions of Yellow-legged Gulls *Larus michahellis atlantis* during the study period. The kernel density is represented by the 95%, 75% and 50% contours, with increasing shading. White points represent at-sea gull locations during the study period.

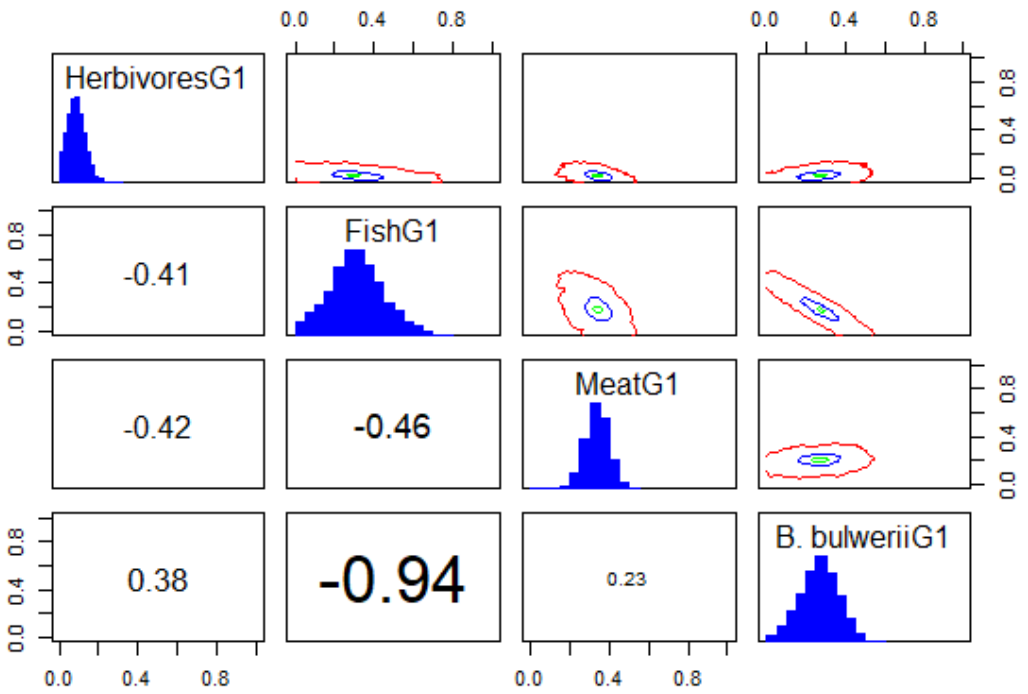

Figure B3 – Matrixplot of the proportions of food categories consumed by adult Yellow-legged Gulls *Larus michahellis atlantis* in Madeira. Terrestrial herbivores (snails, wart-biters and rabbits), Marine fish (Blue Jack Mackerel, Atlantic Chub Mackerel and Common Bogue), Refuse (chicken, pork and cow meat), and Bulwer's Petrel.

Video B4 – Example of the animation of time-matched Yellow-legged Gulls *Larus michahellis atlantis* and fishing vessels movements in the Archipelago of Madeira between April and September 2016. Fishing vessels are represented by black points and gulls by red points. Access: https://bioone.org/journals/ardeola/volume-66/issue-1/arla.66.1.2019.sc4/A-Gull-that-Scarcely-Ventures-on-the-Ocean--Yellow/10.13157/arla.66.1.2019.sc4.short

CHAPTER 5

Credits: Joana Romero

This chapter is published as:

Joana Romero, Paulo Catry, Hany Alonso, José Pedro Granadeiro (2021) Seabird diet analysis suggests sudden shift in the pelagic communities of the subtropical Northeast Atlantic. Marine Environmental Research, 165: 105232.

Seabird diet analysis suggests sudden shift in the pelagic communities of the subtropical Northeast Atlantic

Abstract

The dynamics of the subtropical pelagic ecosystems of the Northeast Atlantic are still poorly known due to the high costs associated with sampling large oceanic areas. Top predators can be used as alternative low-cost samplers and indicators of the temporal variability of such systems. To study the variation in the composition of pelagic species through time in the broad Canary current region, we analysed foraging trips and regurgitations of Cory's shearwaters *Calonectris borealis* nesting on Selvagens Islands, in 2008-2011 and 2016-2018. Fisheries data, oceanographic variables and the North Atlantic Oscillation were explored as possible explanatory variables for trends in behaviour and diet. Cory's shearwaters diet, complemented by fisheries data, revealed marked changes in the composition of the pelagic fish communities. In 2016 there was a peak in the abundance of the Atlantic chub mackerel *Scomber colias*, followed by an explosive increase in the abundance of the Longspine snipefish *Macroramphosus scolopax* in 2017 and 2018, as deduced from the diet composition of the Cory's shearwater, and supported by fisheries data, in the broad oceanic area surrounding the Selvagens Islands. Oceanographic variables did not show fluctuations correlated with these marked shifts in pelagic fish availability, the causes of which remain largely unknown. This study highlights the importance of the Atlantic chub mackerel and of the Longspine snipefish in the Madeira/Canary region and exemplifies the efficiency of avian predators in revealing rapid changes in pelagic communities of oceanic domains. Such trends and variations need to be better monitored and understood to measure the impact of ongoing global changes and to sustainably manage the marine environment and resources.

Keywords: Seabirds, Ecosystem change, Pelagic, Canary Current, *Calonectris borealis*, *Macroramphosus scolopax*, *Scomber colias*, Community shift

Introduction

The high-seas of the subtropical eastern North Atlantic are a nutrient-poor region, contrasting with the richer waters of the strong coastal upwelling of West Africa associated with the Canary current (Cropper et al., 2014). The existence of seamounts and islands in an otherwise deep-ocean region enhances conditions for many pelagic organisms to thrive in this area (Morato et al., 2008; Pitcher et al., 2007).

Even though predators at high trophic levels dominate the pelagic community with a large number of species in this region, all trophic levels are characterized by a low biomass when comparing with the more productive coastal region (Pitcher et al., 2007). Among these forage fish are the Atlantic chub mackerel *Scomber colias* (hereafter simply chub mackerel) and the Blue jack mackerel *Trachurus picturatus* which are some of the most abundant and with higher productivity rates of this type of ecosystem (Hermida and Delgado, 2016). Other vital, but less studied marine organisms, include cephalopods and mesopelagic fish which sustain not only deep-sea fish (Fock et al., 2002a) but also epipelagic feeders, like seabirds (Waap et al., 2017). In addition, their daily vertical migration creates an important link between the depths and the epipelagic domain (Salvanes and Kristoffersen, 2001).

Small pelagic fish have been studied extensively in coastal shelf areas where they often represent commercially important fisheries. In neritic environments, oceanographic variables (e.g. Thiaw et al. 2017) and environmental indexes have been suggested as explanations for the variations and shifts in the reproduction or migration of marine species (e.g. Edwards et al. 2013). The only other pelagic habitat which has been further studied are seamounts (Pitcher et al., 2007). On the other hand, the open ocean beyond shelf waters is among the least known biomes on Earth because of the logistic and monetary challenges of sampling these areas. Data on the ecology and temporal fluctuations of pelagic species in areas such as the oceanic region around the Madeira and Canary archipelagos, off NW Africa, are still very limited. Here, there have been some attempts to study the composition, abundance and distribution of pelagic and demersal species with the help of research or fishing vessels (Christiansen et al., 2009; Delgado et al., 2018; Fock et al., 2002b). However, these studies were mostly species-directed and few presented a multi-specific approach.

Top predators with high mobility, such as cetaceans, tuna, and seabirds, have been successfully used as tools to sample large areas of the marine environment (e.g. Grebmeier

et al. 2006; Pethybridge et al. 2015; Church et al. 2018). Studies on their diet and foraging behaviour enable scientists to gather useful information on the composition and the spatial and temporal distribution of the trophic groups that constitute their prey (Velarde et al., 1994). The Cory's shearwater *Calonectris borealis* has been the target of long-term studies which have provided important information on their feeding ecology and behaviour (e.g. Alonso et al., 2018, 2012). This pelagic seabird nests in several islands of the Macaronesian region, including the Selvagem islands, a small group of oceanic islands ca. 300 km south of the Madeira archipelago. During the breeding season, birds from Selvagem typically travel several hundred kilometres in a single foraging trip, targeting pelagic areas around the island, seamounts and also neritic areas over the African continental shelf (Alonso et al., 2018). They are generalist predators, feeding on a variety of (mostly shoaling) pelagic fish and squid species caught during the day near the surface of the ocean (Alonso et al., 2014; Granadeiro et al., 1998a). Cory's shearwaters are also known to occasionally interact with underwater predators, like tunas and cetaceans, which drive prey to the surface and make them available to seabirds (Veit and Harrison, 2017).

As an abundance and widespread species in this region, these seabirds are potential indicators of important variations in epipelagic communities that might pinpoint changes in the structure of prey communities. In the present study, we describe the interannual variability of the pelagic community in the broad region surrounding the Selvagens islands, using the Cory's shearwater as a biological sampler. We combined dietary information with the location of their main foraging areas and fisheries data in order to assess the temporal variations in the composition and distribution of the most common pelagic species in the region. Concurrently, we examined the changes in oceanographic variables, to assess the extent to which they might explain the variation of the community in this oceanic area. Finally, we examine the relationship between the observed changes in the diet and the potential consequences for the reproductive success of this species.

Methods

Fieldwork was carried out at Selvagem Grande island (30° 09' N, 15° 52' W, Figure 1) where data was collected during the chick-rearing seasons of 2008-2011, and 2016-2018.

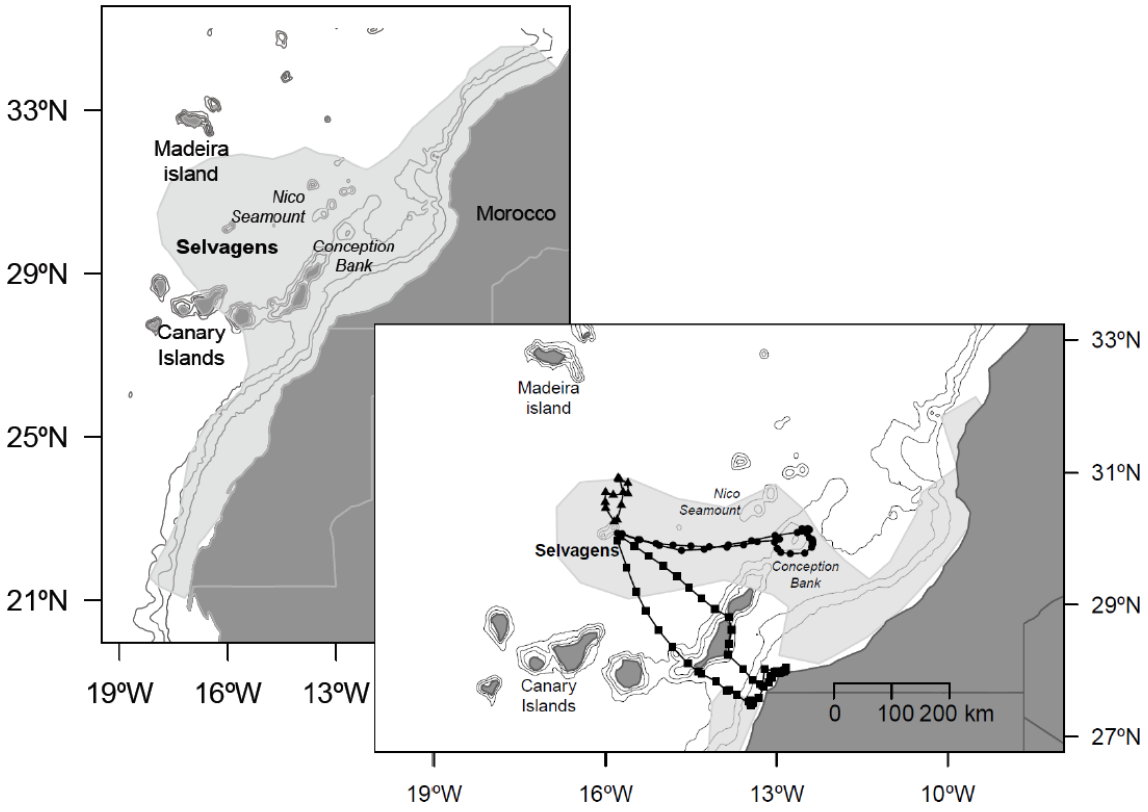

Figure 1 – (A) Foraging areas of Cory's shearwaters *Calonectris borealis* during the breeding season in Selvagem Grande in 2008-2011 and 2016-2018, as revealed by the present study (shadowed area corresponds to 95% Kernel Density Estimation). (B) Domains used by Cory's shearwaters during their foraging trips (shadowed areas correspond to 50% Kernel Density Estimation) and examples of foraging trips to Pelagic areas (▲), Seamounts (●), and the African coast (■). Isobathic lines of 200m, 1000m and 2000m are represented as black lines.

Diet

Sampling and identification of prey

A total of 827 regurgitations were collected between July-late August of 2008-2011 and 2016-2018. Breeding individuals were captured upon their arrival at the nest to feed their chick at dusk and their stomach content was collected by stomach flushing with salt water (Wilson, 1984). Individuals were then marked with colour (livestock paint crayon) to avoid any subsequent disturbance. The stomach content was then carefully sieved to remove excess water and immediately stored in a container and frozen until analysis in the laboratory. Less

digested fish prey were identified morphologically to the lowest taxonomic level, using identification guides. Digested items (levels III and IV, following Alonso et al., 2018) were ascribed to species based on our reference collection of fish skeletons and otoliths from the NE Atlantic (over 700 specimens of ca. 100 species).

Whenever the taxonomic identification of a prey by hard structures was not possible, a muscle tissue sample was collected from the remaining bones, stored in 96% alcohol, and frozen to be identified by DNA barcoding (Alonso et al., 2014). A total of 103 muscle samples belonging to 56 fish and 47 cephalopod prey were collected from Cory's shearwaters regurgitations. DNA was extracted from these samples using the E.Z.N.A. Tissue DNA kit (Omega Bio-tek). The 3' end region of the 16S rRNA gene of fish and cephalopod DNA was amplified with the universal primers 16Sar and 16SSbr (Palumbi, 1996) using optimized PCR conditions (Alonso et al., 2014). The PCR products were sequenced in both directions in outsourcing (Macrogen Inc). The resulting sequences were used in BLAST (NCBI) searches and similarity values higher than 98% were considered as a positive identification for the queried sample.

For the purpose of this study we did not distinguish between different Chub mackerel species and refer to them as *Scomber* sp., as several prey items were only identified to genus level. Nevertheless, only chub mackerel *Scomber colias* was identified to species level within the samples. Eroded cephalopod beaks were not included in the analysis of the diet because they tend to remain in the stomach of seabirds for long periods (weeks) after ingestion, resulting in an over-representation of this group when they are included.

Data analysis

All fish found whole in the regurgitations were weighted (wet weight, ±0.1g) and measured (standard length, ±1mm). Whenever that was not possible, fish size was estimated from the size of specific vertebrae using published equations (Granadeiro and Silva, 2000). The standard length (SL) of Pilotfish was estimated from the length of the first caudal vertebrae (CV); $1^{st}CV$; $SL = 1.602 + 1^{st}CV \times 29.998$, r^2=0.98, n=14 (SL=30–118mm) (H. Alonso, unpubl).

Numeric frequencies (NF, number of individuals of a given prey type as a percentage of the total number of prey items), and frequencies of occurrence (FO, number of samples

with a given prey type as a percentage of the total number of samples) were calculated for each prey species (or lowest taxonomic level identified for a prey item) and year.

A Permutational Multivariate Analysis of Variance (PERMANOVA) was performed to check for significant differences in the diet of the Cory's shearwater among years. The PERMANOVA was carried out using the R *vegan* package with Jaccard similarities on prey presence/absence in regurgitations (FO) (Oksanen et al., 2019). In order to compare the diet diversity of this species among years, the Shannon-Wiener diversity index (*H'*) was calculated for numeric frequency. To avoid bias due to the different number of samples collected in each year, we resampled the smallest number of samples collected (n=30) and carried it out 1000 times for each year. Means and standard deviations were then calculated from those values.

GPS deployment and foraging trip analysis

GPS-loggers were deployed in a total of 150 breeding Cory's shearwaters during the chick rearing season of 2009-2011 (12, 24, and 43 individuals, respectively), 2016 (43) and 2018 (28). The weight of GPS devices (iGotU GPS loggers, 17g) represented ca. 2% of the average weight of an adult Cory's shearwater, therefore unlikely to have deleterious effect on the behaviour of birds (Phillips et al., 2003). GPS loggers were attached to four central tail feathers with TESA tape, and deployed in the nests at dusk, while the adults were visiting the chicks. Upon return from the feeding trip, the bird was recaptured, and the GPS retrieved. Most trips lasted between one and three days (79%, n=306), although some lasted up to 11 days.

Positional data were downloaded from the loggers and divided into separate feeding trips, each starting and ending in Selvagem Island. A total of 306 trips were discriminated from the data. Different GPS loggers were programmed to collect fixes between 10min and 60min intervals. Consequently, in order to allow for comparison among birds, all trips were processed to only include hourly positions, discarding all remaining fixes.

Area utilization was calculated with Kernel Density Estimation (KDE) using the R software package *adehabitatHR* (Calenge, 2015). The home-range and the main foraging areas were considered as those comprising 95% and 50% of the positions, respectively. We compared home ranges and foraging areas of different years using the Utilization Distribution Overlap Index (UDOI), made available through function *kerneloverlap*.

The 50% KDE created by the combination of all trips, revealed 4 main foraging domains: Selvagem (2000m bathymetric line around the Selvagem archipelago); Pelagic (circle with a 160km radius around Selvagem and with depths between 2000 and 4000m); Seamounts (2000m bathymetric line around the seamounts) and African coast (area defined by latitudes 20-35˚N and 80km offshore) (Alonso et al., 2018, 2012) (Figure1B). Due to different oceanographic conditions, the African Coast area was further subdivided into Strong Permanent Upwelling Region (SUR, 20-26˚N) and Weak Permanent Upwelling Region (WUR, 26-35˚N) (Cropper et al., 2014), creating five domains with different environmental features. One of these domains was assigned to each feeding trip as its destination. The destination was assigned as the domain with the highest number of positions of that trip (and the most convoluted part of the track), which was usually also the area with the farthest locations from the colony. Birds sometimes crossed more than one oceanographic domain, but one of these was much more used than the others.

The frequency of occurrence of each foraging domain was calculated to quantify its use by Cory's shearwaters each year. Permutational multivariate analysis of variance (PERMANOVA) was used to test for interannual variability in foraging areas and was carried out using the *vegan* package with Jaccard similarities on destination of each foraging trip (Oksanen et al., 2019). To calculate the maximum distances from the colony reached by each individual, distances between each position and Selvagem were calculated using the function *spDistsN1* from the package *sp* (Pebesma et al., 2018). Differences among years in maximum distances from the colony were tested using a one-way ANOVA. All statistical analyses were performed using the Software R (version 3.5.2).

Fisheries and environmental data

The total annual landings of chub mackerel from Madeira Island from local purse-seiners were obtained from the Regional Direction of Fisheries of the Autonomous Region of Madeira and used as an indicator of the abundance of this species between 2008 and 2018.

Monthly 4km AQUAMODIS Chlorophyll a (Chla) and SST data were downloaded from the ERDDAP data server (https://coastwatch.pfeg.noaa.gov/erddap/index.html). Monthly 0.125˚ zonal (u) and meridional (v) wind components at 10 meter were downloaded from the European Centre for Medium-Range Weather Forecasts (ECMWF) using the ERA-Interim server (https://apps.ecmwf.int/datasets/). The NAO index was obtained from the

Climate Data Guide server (https://climatedataguide.ucar.edu/climate-data/hurrell-north-atlantic-oscillation-nao-index-station-based). Data on these variables were obtained for January to April (hereafter "Winter", corresponding to the strongest period of upwelling off the African coast and, thus, the highest Chl a values) and June to September (hereafter "Summer", corresponding to our study period and second peak in Chl a) between 2008-2018, to assess seasonal and interannual variability (Davenport et al., 1999). Each variable was averaged within the domains. To do that, the median value of each month was obtained for each domain, and then we calculated the mean for each season. Mean Chl a values were then log transformed for further analysis. Climatic (NAO) and environmental (Chl a, SST, Wind speed and direction) variables were analysed for correlation with the prey occurrence and with the frequency of occurrence of Cory's shearwaters in different domains throughout the study period. Analyses of variance (ANOVAs) were performed to assess differences among years, seasons and domains.

Breeding success

Throughout the breeding seasons of 2008-2011 and 2016-2018, in Selvagem Grande, between 296 and 349 breeding pairs of Cory's shearwaters were followed each year as part of a long-term demographic study. Successes and failures were registered and the hatching success (percentage of laid eggs that hatched; Cory's shearwaters lay one single egg per year), fledging success (percentage of hatched chicks that survived to fledging age), and the breeding success (hatching success × fledging success= percentage of chicks fledged per egg laid) were calculated as a measure of reproductive performance.

Results

Foraging ecology of the Cory's shearwater

We counted a total of 2775 prey individuals in regurgitations, 79% of which were successfully identified to species, genus or family level, resulting in 47 identified species/genus of 32 identified families (see Supplementary Materials, Table A.1). Fish were the most consumed prey across all years, both in terms of number of individuals (NF range = 68.7-99.2%) and in occurrence (FO range = 87.1-100%). Cephalopods were always present throughout the study period (NF range = 0.8-26.7%; FO range = 10.0-50.0%) (see Supplementary Materials, Table A.1). Overall, chub mackerel was the most common prey found in the regurgitations of Cory's shearwater from 2008 to 2011 and in 2016, followed

by Pilotfish *Naucrates ductor*, European pilchard *Sardina pilchardus* and Flying-neon squid *Ommastrephes bartramii* (Figure 2). In 2017, Longspine snipefish *Macroramphosus scolopax* appeared as the most numerous prey (NF=61.5%, Figure 2), occurring in 53% of the samples. This situation persisted in 2018 with snipefish dominating the diet (NF=95.3% and FO=87.5%). We found significant differences between years in the diet composition of this shearwater (PERMANOVA: $F_{6,820} = 13.202$, $r^2 = 0.08$, $p<0.01$).

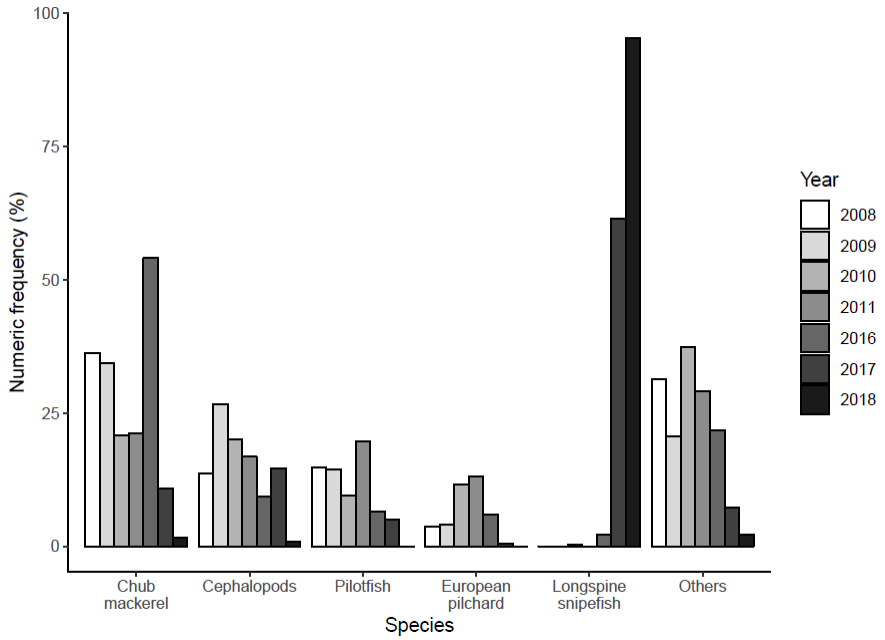

Figure 2- Interannual variability (numeric frequency) of the most common prey of the Cory's shearwater *Calonectris borealis* from Selvagem Grande (2008, n=471; 2009, n=703; 2010, n=633; 2011, n=137; 2016, n=183; 2017, n=156; 2018, n=492). Detailed data in Supplementary Materials, Table A.1.

In 2017 and 2018 the Shannon-Wiener diversity index reduced abruptly to H=1.36±0.24 and H=0.24±0.05, respectively, compared with the previous years' mean ranges: H=2.19-2.61 in 2008-2011, and H=1.75±0.20 in 2016.

The average standard length of the Longspine snipefish was 78.5mm (range:51.7-115.9mm, n=516), with no differences among the 3 years (ANOVA: $F_{2,512}=0.92$, p=0.39, See Supplementary materials, Figure A.1). Cory's shearwater fed on Pilotfish with standard lengths of 90.7mm (range: 24.3-225.6mm). See Supplementary materials for further information on the standard length of prey of Cory's shearwaters (Table A.2).

The destination of foraging trips also presented important differences among years (PERMANOVA: $F_{5,300} = 11.73$, $r^2 = 0.16$, $p<0.01$, Figure 3). From 2009 to 2011, the African coast was the most used foraging destination (52±11%). However, in 2016, most trips targeted the Selvagem domain and its surroundings (FO=28% and FO=36%, respectively), and in 2018, the Pelagic domain was the most frequently used (FO=82%). Overall, trips in 2016 and 2018 were closer to the colony comparing to other years, presenting average maximum distances from the colony of 121.6 and 91.6km, respectively. Even though, 2016 presented a higher number of shorter trips than in 2018. Trips from 2016 and 2018 were significantly different from trips from 2010, 2011 and 2013 (ANOVA: $F_{5,312}=12.21$, $p<0.01$ followed by post-hoc test Tukey HSD, Figure 4).

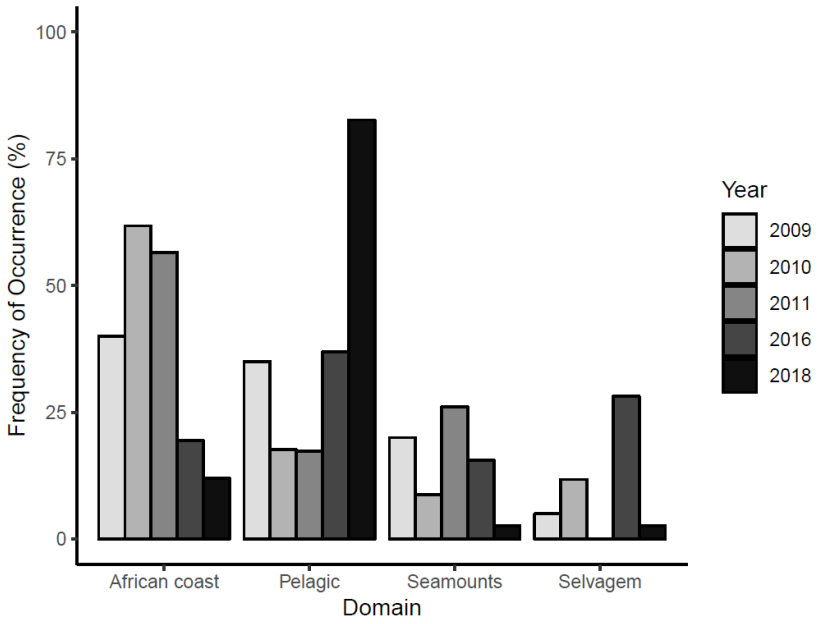

Figure 3 - Percentage of use of different oceanic domains (FO%) by Cory's shearwaters *Calonectris borealis* during the chick-rearing phase of 2009-2011 (*n*=20, 34, 46, 28, respectively), 2016 (*n*=103), 2018 (*n*=75). Data from Weak Permanent Upwelling Region and Strong Permanent Upwelling Region were combined ("African coast").

The total annual landings of chub mackerels in the archipelago of Madeira from 2008 to 2018 showed no down trend that could imply a reduction in the availability of the species (Figure 5). It is worth noting that in 2018, when this fish almost disappeared from the diet of Cory's shearwaters, catch levels by human fisheries were not unusually low (Figure 5). The

correlation between the numeric frequency of chub mackerels and landings showed to be positive but not quite attaining statistical significance (r=0.63, p=0.13).

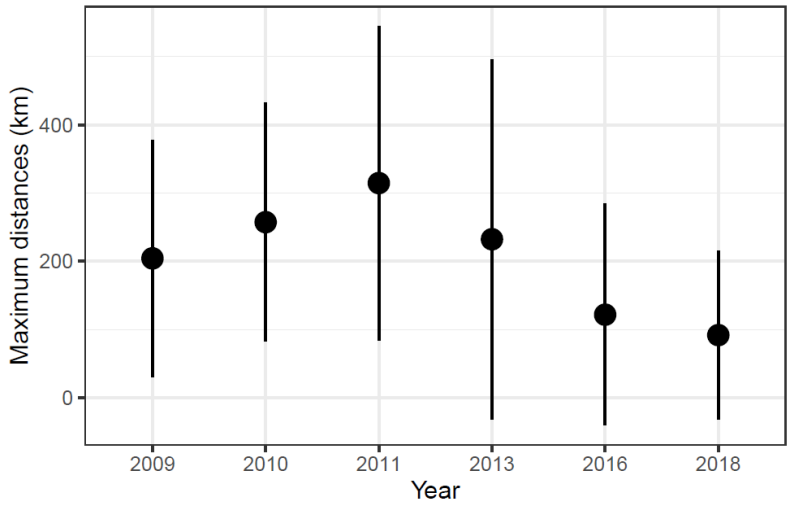

Figure 4 - Average (SD) maximum distance (Km) reached by Cory's shearwaters *Calonectris borealis*, in each trip per year.

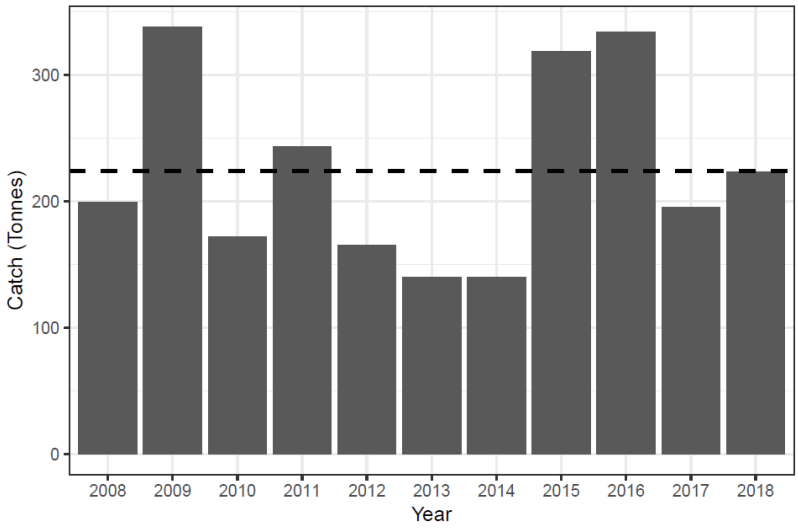

Figure 5 - Variation in the total annual landings and mean catch value (224 tonnes, dashed line) of Atlantic chub mackerel *Scomber colias* in Madeira island for the decade of 2008-2018.

Environmental and oceanographic characteristics of foraging areas

Overall, the defined domains showed a similar annual pattern in the SST, Chl a and wind components, but their mean values differed, except the Selvagem and Pelagic domains

which were indistinguishable (see Supplementary Materials, Table A.3 and Figure A.2). No correlation was found between any of the oceanographic and meteorological (NAO) variables studied and the proportions of various prey in the diet of Cory's shearwaters (see Supplementary Materials, Table A.4) either in Winter or Summer.

Breeding success

Breeding success only varied slightly during the studied period of 2008-2011 (72.1-75.4% in 2008-2010 and 63.8% in 2011) and 2016-2018 (71.3-76.7%).

Discussion

Cory's Shearwaters are opportunistic feeders which used different foraging domains within our study area, ranging far from their breeding colony (Figure 1, see also Alonso et al., 2018). We took advantage of this to gather information on prey in these waters for a total of 7 years using the combination of GPS-tracking and diet data, which provided useful indications concerning the likely origin of their pelagic prey (Alonso et al., 2018). In 2016, the population of chub mackerel showed a peak of abundance in the waters surrounding Selvagens. More noticeably, since 2017 Longspine snipefish suddenly became the dominant prey-item of Cory's shearwaters, mostly captured in the pelagic domain adjacent to Selvagens islands. Fisheries data indicate that the dietary shift of this seabird was not associated with any noticeable decrease of chub mackerel in the region. Hence, our Cory's shearwater diet dataset strongly suggests a major shift in the epipelagic fish communities of this little-known region, with a sudden and dramatic expansion of a previously scarce species, the Longspine snipefish.

From 2008 to 2011, the main prey of Cory's shearwaters from Selvagem Grande colony was the chub mackerel. Chub mackerels are widely distributed in the NW African region, in deep-sea areas, seamounts, and continental and island shelves (Alonso et al., 2018; Pitcher et al., 2007; Stromme et al., 2006; Wienerroither et al., 2009). Such large distribution might explain its importance in the diet of Cory's shearwaters (Alonso et al., 2018). A positive correlation (which failed to reach significance, possibly due to the small number of sampled years) between the landings of chub mackerel and its numeric frequency supports the hypothesis that the diet of Cory's shearwaters may provide broad indication of the abundance of this species. However, it would be important to sample more years and for a longer period of time to validate this assumption. While it is difficult to know where chub mackerels are

most abundant, it is possible to state that they were very abundant in the Selvagem domain in 2016. In this year, Cory's shearwaters frequently foraged around Selvagem Grande (FO%=28%) and adjacent pelagic waters (FO%=36%) and fed mostly on chub mackerels (NF=55% and FO=70%). The peak in total annual landings of chub mackerels observed in Madeira (this study) and in the African coast (Morocco to Senegal, including the Canary islands, 400000 tonnes; FAO, 2018) in that same year fit well with the peak that we recorded around Selvagem islands. The increase of the population at that time is further confirmed by acoustic surveys performed along the African coast in 2016-2017 (FAO, 2019).

From 2009 to 2011, the African coast was the domain where Cory's shearwaters foraged the most. There, the community of forage fish is mainly composed by European pilchards, which represent 45% of catch contribution of small pelagic fish (FAO, 2018). From 2008 to 2010, there was a slight increase in the total annual catches of the European pilchard (FAO, 2018) which coincides with the increase of European pilchards in Cory's shearwater diet. In 2016, the proportion of pilchards in the diet did not follow the new increase of landings described in FAO (2018). This can be explained by a reduction in the use of the African coast by Cory's shearwaters due to the apparent increase of chub mackerel around Selvagem.

Pilotfish which are generally found in association with floating structures (juveniles) or large marine species (adults) in pelagic ecosystems (e.g. Riera et al. 1999), were also a common pelagic prey of Cory's shearwaters. Throughout the period of 2008-2011 and 2016-2017, this seabird preyed upon Pilotfish with sizes between 24 and 230mm, which correspond to juveniles of up to 5 month old (Vassilopoulou et al., 2005). The near-constant presence of this age-group in the diet of Cory's shearwaters during this period is an indicator that they were feeding on new recruits every year.

Besides fish, cephalopods were also an important prey group in the diet of the Cory's shearwater. In our study, 30% of the cephalopods found in the stomachs of this seabird were Neon-flying squid *Ommastrephes bartramii* or belonged to the *Ommastrephidae* family. This is the most common cephalopod family in the Canary Current System, and the Neon-flying squid is among the most common species off North Africa (Hastie et al., 2009). The small variation in the occurrence of flying squids in the diet of the Cory's shearwater in the study

years of 2008-2017 indicates a regular presence of this species in the pelagic waters off NW Africa.

In 2017, Cory's shearwaters from the Selvagem colony shifted their diet to feed mostly on Longspine snipefish. In the following year, the importance of this fish in the diet of this seabird further increased to 95.3%, and the pelagic areas around the archipelago of Selvagens replaced the Selvagem domain and adjacent waters as the main foraging grounds of the Cory's shearwater. The high abundance of the chub mackerel in the African coast and the Canary islands, in 2017 and 2018 (FAO, 2019) implies that the consumption of the Longspine snipefish was not a result of a shortage of the traditional prey, but a choice. Therefore, we conclude that the trophic shift observed for this seabird reflects an increase in the availability of Longspine snipefish in the pelagic waters around Selvagem in 2017/2018. Such an increase very close to the nesting colony probably allowed Cory's shearwaters to have access to high quantities of food with low effort, even if less caloric (Martins et al., 2004), rather than targeting alternative, more nutritious prey farther away, which agrees with the classic optimal foraging theory and central place foraging (Bartumeus and Catalan, 2009). Thus, should Longspine snipefish have been abundant close to the colony in previous years, then these seabirds would not have travelled to the African coast to forage. Despite the possible link between a change in the foraging area and a shift in prey consumed, the foraging behaviour of seabirds is known to be influenced by extrinsic factors that are related to prey availability and not by a random choice of foraging areas (Shealer, 2002). Furthermore, between 2016 and 2018, the foraging areas remained the same but with a shift in the diet of Cory's shearwaters from chub mackerels to snipefish, which suggests that the foraging area was not the reason for the shift in diet. For this reason, the shift in the diet is much more likely to be a result of the shift in the prey community of that specific area than solely a change in the foraging area.

Snipefish found in the regurgitations of Cory's shearwater had a mean length of 78.5±59.1mm, which did not vary during the study years. These sizes correspond to snipefish slightly younger than one year (Ehrich, 1976; Lopes and Farinha, 1996), possibly resulting from the spawning of December-March (Lopes and Farinha, 1996). The yearly occurrence of snipefish with these standard lengths in the diet of the Cory's shearwater allows us to conclude that the birds were preying on new recruits every year which, consequently, leads

us to hypothesize that snipefish were reproducing successfully in the region from 2016 to 2018.

The distribution of the Longspine snipefish in the North Atlantic ranges in latitude from the Iberian Peninsula down to North Mauritania, including varied environments such as shelves and upper slopes, and seamounts (Ehrich et al., 1987). Marked fluctuations in Longspine snipefish abundance have been recorded in other regions of the NE Atlantic. On the Portuguese continental shelf, the only area monitored regularly through systematic surveys (Borges, 2000; Lopes et al., 2006; Lopes and Farinha, 1996; Marques et al., 2005), the snipefish population presented high abundances in the 1970's (annual landings: 10,000 tonnes in 1973, and 33,000 tonnes in 1978) (Morais, 1981), and late 1990's/ early 2000's (acoustic estimates: 500 000 tonnes in 1998 to 175 000 tonnes in 2003) (Marques et al., 2005), with low abundances in the 1980's (Marques et al., 2005). Seemingly, these fluctuations coincided with abrupt fluctuations in other areas. Outbursts were described in the coast of Morocco (Arístegui et al., 2004) and in the Azores (Granadeiro et al., 1998; Ramos et al., 1998) in the 70's (acoustic survey: 1,000,000 tonnes in 1976 to disappear in the 80's) and the 90's (1994-1995), respectively. In 2005, dietary data from Cory's shearwaters provided some evidence of the decrease in abundance of snipefish in the Azores comparing with the 90's (Xavier et al., 2011). The Longspine snipefish was considered abundant in the Seine Seamount (located northeast of Madeira) in 2003-2005, and in the Meteor Seamount (located in the middle of the Atlantic, west of Madeira) in 1967, 1970 and 1998 (Christiansen et al., 2009; Fock et al., 2002b; Zidowitz and Fock, 2004).

Studies have shown that the appearance and disappearance of Longspine snipefish throughout time can alter considerably the trophic web, with predators suddenly shifting their diet to this prey once its numbers increase (e.g. Morato et al. 1999; Silva 1999). Snipefish is an important prey (at some times and locations the main prey) of seabirds, sharks, dolphins, tunas, rays, hakes and John Dory *Zeus faber* (e.g. Granadeiro et al. 1998; Morato et al. 1999, 2003; Silva 1999; Zidowitz and Fock 2004). To what extent snipefish can influence the functioning of the ecosystems when their numbers change is still uncertain. In our study, Cory's shearwaters, which like many seabird species are sensitive to prey fluctuations (Becker et al., 2007; Kowalczyk et al., 2014), did not show signs of having been affected by this major shift in their main prey. Despite a radical shift in diet, between 2016 and 2018, the

breeding success remained largely unchanged. This also suggests that snipefish can be a valuable resource for pelagic predators.

What drives the Longspine snipefish wide population fluctuations is still unknown, and we did not find changes in oceanographic variables that correlated with the increase of this species' abundance reported here. The sudden proliferation of some marine taxa can sometimes be associated with the disappearance of a dominant species (predators or competitors) due to fisheries or environmental changes (Caddy and Rodhouse, 1998; Gulland and Garcia, 1984). The increase of snipefish in our study was apparently not linked with the decrease of any other abundant species, according to fisheries data (FAO, 2019). So, the reasons for such successful consecutive recruitments is yet to be discovered.

The Cory's shearwater is considered to be a generalist predator, but it is important to point out that Cory's shearwaters are surface feeders and shallow divers, reaching an average depth during foraging trips of only 2.7m (Mougin and Mougin, 1998). Hence, they cannot be considered totally unbiased samplers of the whole marine environment. Their diet will thus reflect availability in surface waters, rather than overall abundance of fish stocks. Nevertheless, it is reasonable to assume that availability in surface waters correlates with overall abundance, even if imperfectly so. The action of subsurface predators can bring more prey to surface waters, and should their abundance drastically change, this could have an important influence in the diet of Cory's shearwaters. However, we know of no evidence for drastic changes in the community of underwater predators which might explain the very major shift in the diet of the Cory's shearwaters observed in this study.

This study exemplifies how biological samplers like Cory's shearwaters can provide novel information about important changes in epipelagic ecosystems, that would otherwise be difficult to detect. Previous studies have already shown the usefulness of seabirds as bioindicators of their foraging areas and prey, unveiling annual fluctuations of fish stocks (e.g. Scopel et al., 2018) and changes in the food web and in oceanographic conditions (e.g. Montevecchi, 2007). The major shifts in the epipelagic fish community around Selvagens archipelago revealed by this study and the lack of known environmental correlates for such shifts underscore our poor understanding of the dynamics of key-species in little known subtropical pelagic waters. Such trends and variations need to be better monitored and

understood if we are to measure the impact of ongoing global changes and to sustainably manage the broad marine environment and resources.

Acknowledgements

This work was supported by Fundação para a Ciência e a Tecnologia (FCT Portugal) through the project Oceanwebs (PTDC/MAR-PRO/0929/2014) and Seamigrant (PTDC/BIA-ANM/3743/2014), the strategic projects UIDB/04292/2020 and UIDP/04292/2020 granted to MARE, and UIDB/50017/2020 and UIDP/50017/2020 granted to CESAM. PD/BD/127810/2016 was granted to JR by FCT. We would like to acknowledge Serviço do Parque Natural da Madeira and Instituto das Florestas e Conservação da Natureza, specially Dr. Paulo Oliveira and Dr. Carolina Santos, for providing the required permits to undertake experiments with birds and logistical support to carry out the work at the islands of Selvagens. All procedures were carried out following a positive recommendation from the Animal Welfare Regulatory Body of the Faculty of Sciences of Lisbon University and were carried out under licenses issued by the Direção Geral de Alimentação e Veterinária, license number DGAV 0421/2016. Thanks are due to Direção Regional de Pescas da Madeira, specially to Dr. Graça Faria, for providing data on the annual landings of small pelagic fishes. Filipe Moniz for helping during the field and laboratory work. We also thank to Letizia Campioni, Diana Barão, Teresa Catry, Maria Alho and Marie Claire for helping during field work and giving further insights for this study, and to park-wardens Carlos Clemente, Carlos Santos, Jaques da Mata, João Paulo Mendes, Maurício Baptista, Marco Camacho and Fernando. No conflicts of interest.

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Supplementary Materials

Table A.2 - Numeric frequency (NF%, number of prey in parenthesis) and Frequency of occurrence (FO%, number of samples in parenthesis) of prey species found in the regurgitations of Cory's shearwaters Calonectris borealis during the chick rearing season of 2008-2011 and 2016-2018, in Selvagem Grande island.

Prey Species	NF%							FO%						
	2008 (471)	2009 (703)	2010 (633)	2011 (137)	2016 (183)	2017 (156)	2018 (492)	2008 (199)	2009 (278)	2010 (194)	2011 (38)	2016 (48)	2017 (30)	2018 (40)
TELEOSTEI	**84.1**	**72.3**	**68.7**	**83.2**	**88.5**	**84.6**	**99.2**	**89.9**	**87.1**	**89.7**	**97.4**	**95.8**	**90**	**100**
Belonidae														
Belone belone				1.5	0.5						5.3	2.1		
Belone sp	0.8	0.1	1.4					2.0	0.4	3.6				
Caproidae														
Capros aper			0.2							0.5				
Carangidae														
Naucrates ductor	14.9	14.4	9.6	19.7	6.6	5.1		15.1	16.9	13.4	28.9	4.2	6.7	
Trachurus picturatus	0.2	0.1			1.6		1.8	0.5	0.4			4.2		12.5
Trachurus sp	1.1	1.7	3.5	1.5	4.4			2.5	3.2	4.6	5.3	8.3		
Unidentified	0.2	0.4	0.5					0.5	1.1	1.0				
Centriscidae														
Macroramphosus scolopax			0.3		2.2	61.5	95.3			1.0		4.2	53.3	87.5
Clupeidae														
Sardina pilchardus	3.8	4.0	11.7	13.1	6.0	0.6		7.5	8.6	20.1	18.4	10.4	3.3	
Sardinella sp		0.1							0.4					
Unidentified	0.4	0.4	0.6					1.0	1.1	2.1				
Coryphaenidae														
Coryphaena equiselis		0.1			0.5				0.4			2.1		
Coryphaena hippurus				0.7							2.6			

Coryphaena sp	0.2		0.2				0.5		0.5			
Diretmidae												
Diretmus argenteus			0.6						2.1			
Engraulidae												
Engraulis encrasicolus	0.8	3.6	0.5	2.2			1.5	3.2	1.0	5.3		
Exocoetidae	7.6	4	2.7	0.7	1.6		13.1	7.1	7.7	7.9	6.3	
Cheilopogon exsiliens		0.4						1.1				
Cheilopogon melanurus		0.1						0.4				
Cheilopogon pinnatibarbatus		0.3						0.7				
Cheilopogon sp	0.6	0.3	0.3				1.5	0.7	1.0			
Exocoetus volitans	0.6				1.1		1.5				4.2	
Exocoetus sp	3.4	0.4	1.6	0.7			7.0	1.1	5.2	2.6		
Unidentified	3.0	2.4	0.8		0.5		6.0	4.0	2.6		2.1	
Halosauridae												
Unidentified	0.6	0.1	0.2	0.7			1.0	0.4	0.5	2.6		
Microstomatidae												
Nansenia sp				0.7						2.6		
Molidae												
Ranzania laevis			1.1						3.6			
Myctophidae												
Diaphus splendidus		0.1						0.4				
Lampadena luminosa			0.2						0.5			
Unidentified	0.6		0.8	1.5	0.5	1.9	1.5		2.1	5.3	2.1	6.7
Neoscopelidae												
Neoscopelus macrolepidotus	0.2			1.5			0.5			2.6		
Nettastomatidae												
Nettastoma melanurum				0.7						2.6		
Opisthoproctidae												
Opisthoproctus soleatus				0.7						2.6		

Scombridae														
Auxis rochei		0.6					0.4		1.4					5.0
Katsuwonus pelamis	0.2	0.6	0.9					0.5	1.4	3.1				
Scomber colias	16.6	16.1	4.6	9.5	32.2	10.3	1.6	23.6	29.5	10.8	23.7	54.2	46.7	20.0
Scomber sp	19.7	18.2	16.3	11.7	21.9	0.6		30.2	28.4	30.4	26.3	45.8	3.3	
Scomber	36.3	34.3	20.9	21.2	54.1	10.9	1.6	45.7	47.5	35.1	39.5	68.8	50.0	20.0
Scomberesocidae														
Scomberesox saurus						0.6							3.3	
Scomberesox sp	4.2	0.4	2.7		1.1			3.0	1.1	4.6		2.1		
Sparidae														
Boops boops		0.1	0.5		4.9				0.4	1.0		4.2		
Dentex macrophthalmus				7.3							5.3			
Sternoptuchidae														
Argyropelecus aculeatus	0.4							0.5						
Synaphobranchidae														
Unidentified	0.4	0.3	1.3	2.2				1.0	0.7	3.6	7.9			
Trichiuridae														
Unidentified	1.9	0.9	1.6		0.5	0.6		4.5	2.2	4.6		2.1	3.3	
Unidentified Fish	8.9	5.8	7.0	7.3	3.8	3.2		19.6	14.4	20.6	23.7	12.5	13.3	
CEPHALOPOD	**13.6**	**26.7**	**20.1**	**16.8**	**9.3**	**14.7**	**0.8**	**26.6**	**36.7**	**45.9**	**50**	**27.1**	**33.3**	**10**
Chiroteuthidae														
Chiroteuthis sp		0.4							1.1					
Cranchiidae														
Taonius pavo	0.2		0.5					0.5		1.0				
Grimalditeuthidae														
Grimalditeuthis bonplandi	0.2							0.5						
Histioteuthidae														
Histioteuthis arcturi	0.4	0.4	1.9					1.0	1.1	5.7				
Histioteuthis meleanogroteuthis			0.2						0.7	0.5				

Histioteuthis sp	0.4	0.3						1.0						
Unidentified				3.6	1.6						13.2	6.3		
Mastigoteuthidae														
Mastigoteuthis sp		0.1							0.4					
Unidentified			0.6							2.1				
Neuteuthidae														
Neoteuthis sp			0.2							0.5				
Octopoteuthidae														
Taningia danae	0.2	0.1						0.5	0.4					
Ommastrephidae	4.5	10.2	2.4	4.5	1.1	9.0		9.5	15.1	6.2	18.4	4.2	16.7	
Ommastrephes bartramii	3.8	10.0	2.4	1.5		9.0		8.0	14.7	6.2	5.3		16.7	
Unidentified	0.6	0.3		5.1	1.1			1.5	0.7		15.8	4.2		
Onychoteuthidae														
Ancistrotheuthis lichtensteinii		0.1							0.4					
Sepiidae														
Unidentified			0.2							0.5				
Unidentified Cephalopod	7.6	14.9	14.2	6.6	6.6	5.8	0.8	15.6	26.3	35.1	23.7	22.9	20.0	10.0
CRUSTACEA	**2.3**	**0.9**	**11.2**	**0**	**2.2**	**0.6**	**0**	**2.5**	**1.8**	**14.4**	**0**	**6.3**	**3.3**	**0**
Decapoda			0.3							0.5				
Isopoda		0.6	9.8		1.1				1.1	10.8		4.2		
Unidentified Crustacea	2.3	0.3	1.1		1.1	0.6		2.5	0.7	3.1		4.2	3.3	

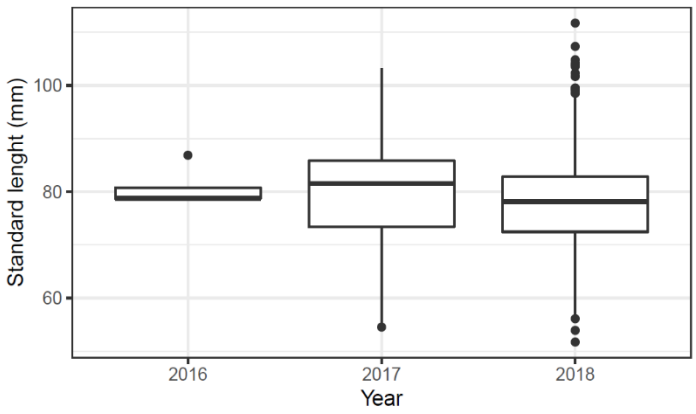


Figure A.1 - Size distribution of the Longspine snipefish *Macroramphosus scolopax* captured by the Cory's shearwater *Calonectris borealis* of Selvagem Grande breeding colony from 2016 to 2018 (2016, *n*=4; 2017, *n*=96; 2018, *n*=469).

Table A.3 - Mean standard length (±SD) and range values (in mm) of each prey species and sampling years of Cory's shearwater *Calonectris borealis* breeding in Selvagem Grande.

Prey	Year	N	Mean	SD	Range
Fish					
Belone belone	2016	1	421.2		
Belone sp.	2008	1	415.7		
	2009	1	408.6		
	2010	6	402.1	13.9	383.9-422.8
Boops boops	2009	1	205.5		
	2010	3	124.6	44.7	93.6-175.9
Capros aper	2010	1	57.4		
Cheilopogon exsiliens	2009	3	268.2	12.8	254.0-279.0
Cheilopogon malanurus	2009	1	212.8		
Cheilopogon pinnatibarbatus	2009	1	249.8		
Cheilopogon sp.	2008	3	205.9	71.9	128.2-270.0
	2009	2	226.3	32.2	203.5-249.0
	2010	2	124.7	41.9	95.1-154.3
Engraulis encrasicolus	2008	2	128.7	4.9	125.2-132.2
	2009	20	141.6	8.1	125.2-156.2
	2010	2	140.4	10.9	132.7-148.1
Exocoetidae	2008	8	219.7	28.9	152.6-249.8
	2009	11	194.1	37.6	114.0-226.7
	2010	3	234.1	18.5	213.7-249.8
Exocoetus sp.	2008	14	216.1	5.3	209.0-228.2
	2009	3	219.8	10.2	221.0-231.0
	2010	9	229.9	12.9	213.7-249.8
	2016	2	214.3	2.6	212.4-216.1

Exocoetus volitans	2008	2	225.7	7.9	220.0-231.3
	2016	2	214.3	2.6	212.4-216.1
Macroramphosus scolopax	2010	1	115.9		
	2016	4	80.8	4.1	78.8-86.9
	2017	75	79.7	10.2	54.6-103.2
	2018	436	78.2	9.2	51.7-111.7
Naucrates ductor	2008	61	103.0	27.2	51.8-225.6
	2009	94	89.2	29.2	24.3-168.4
	2010	59	78.5	27.9	35.7-157.0
	2011	24	97.9	32.9	28.4-204.3
	2016	11	98.8	22.7	60.6-133.1
	2017	6	64.4	14.0	48.9-81.9
Sardina pilchardus	2008	10	192.6	31.5	130.0-234.3
	2009	16	199.3	30.0	135.5-225.4
	2010	50	164.2	23.6	112.1-252.0
	2011	13	123.4	32.8	73.4-185.9
	2016	9	128.0	41.4	89.9-179.2
Scomber sp.	2008	148	185.2	30.4	89.2-270.1
	2009	209	208.1	21.5	162.8-273.3
	2010	102	197.2	18.3	155.0-253.1
	2011	21	214.0	20.7	187.3-270.4
	2016	80	193.7	27.8	155.3-272.5
	2017	9	209.6	31.2	151.4-243.1
	2018	4	227.3	26.4	207.9-266.1
Trachurus picturatus	2008	1	169.4		
	2009	1	217.0		
	2016	3	158.9	7.5	150.8-165.4
	2018	8	153.8	3.7	145.9-157.3
Trachurus sp.	2008	4	229.4	64.6	151.1-309.3
	2009	10	156.4	48.0	76.2-240.2
	2010	19	163.7	17.7	135.4-201.8
	2011	1	291.2		
	2016	4	162.9	19.7	145.9-189.8
Cephalopods					
Grimalditeuthis bonplandi	2008	1	82.2		
Histioteuthis arcturi	2008	2	59.7	18.8	46.4-73.0
Ommastrephes bartramii	2008	18	71.2	29.8	28.0-108.9
	2009	56	54.6	24.4	14.9-109.1
	2010	8	58.4	28.4	20.0-105.0
	2011	2	38.0	24.0	21.0-55.0
	2017	2	75.5	0.7	75.0-76.0
Ommastrephidae	2008	1	63.5		
	2009	1	65.6		
	2011	2	22.0	1.4	21.0-23.0
	2016	1	102.0		
Taonius pavo	2008	1	380.9		

Table A.3 - ANOVA results for differences in oceanographic variables among different domains (Selvagem, Pelagic, Seamounts, Strong Permanent Upwelling Region and Weak Permanent Upwelling Region) in Summer and Winter. Significant differences are marked in bold.

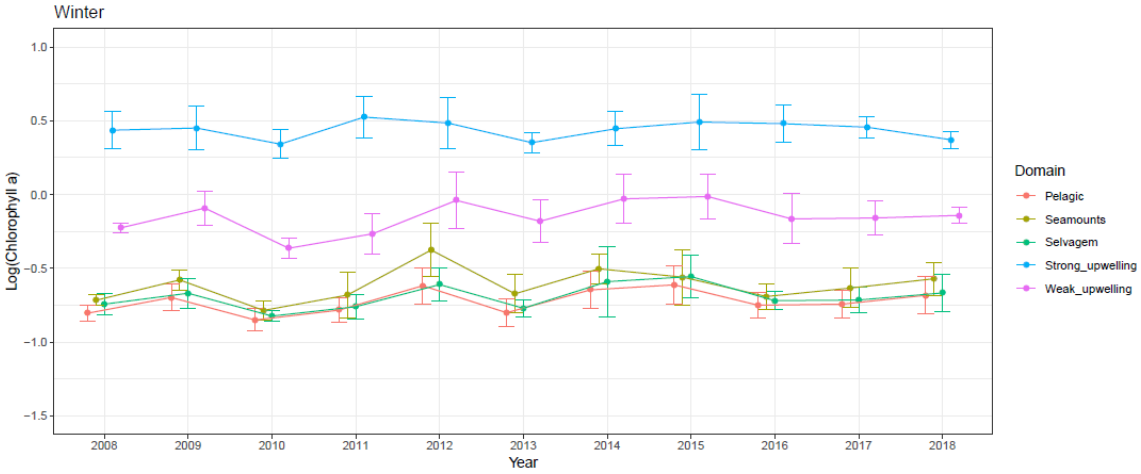
	Domains		Year		Domains x Year	
	ANOVA	p-value	ANOVA	p-value	ANOVA	p-value
Summer						
Chlorophyll a	$F_{4,165}$=2379.879	**<0.01**	$F_{10,165}$=8.851	**<0.01**	$F_{40,165}$=1.797	**<0.01**
Sea Surface Temperature	$F_{4,165}$=30.589	**<0.01**	$F_{10,165}$=1.250	0.263	$F_{40,165}$=0.239	1
Wind speed	$F_{4,165}$=10.349	**<0.01**	$F_{10,165}$=3.088	**<0.01**	$F_{40,165}$=0.253	1
Zonal velocity	$F_{4,165}$=19.337	**<0.01**	$F_{10,165}$=3.219	**<0.01**	$F_{40,165}$=0.427	0.998
Meridional velocity	$F_{4,165}$=13.334	**<0.01**	$F_{10,165}$=3.448	**<0.01**	$F_{40,165}$=0.253	0.999
Winter						
Chlorophyll a	$F_{4,165}$=715.005	**<0.01**	$F_{10,165}$=7.649	**<0.01**	$F_{40,165}$=0.691	0.915
Sea Surface Temperature	$F_{4,165}$=31.637	**<0.01**	$F_{10,165}$=21.608	**<0.01**	$F_{40,165}$=0.761	0.844
Wind speed	$F_{4,165}$=18.633	**<0.01**	$F_{10,165}$=5.253	**<0.01**	$F_{40,165}$=0.238	1
Zonal velocity	$F_{4,165}$=8.202	**<0.01**	$F_{10,165}$=7.372	**<0.01**	$F_{40,165}$=0.368	1
Meridional velocity	$F_{4,165}$=13.575	**<0.01**	$F_{10,165}$=4.944	**<0.01**	$F_{40,165}$=0.370	1

Table A.4 – Pearson's correlation between the oceanographic variables in the Pelagic domain (circle with a 160km radius around Selvagem and with depths between 2000 and 4000m, see text) and the numeric frequency of the main prey in the Cory's shearwater diet. Winter: January-April, Summer: June-Septembeer.

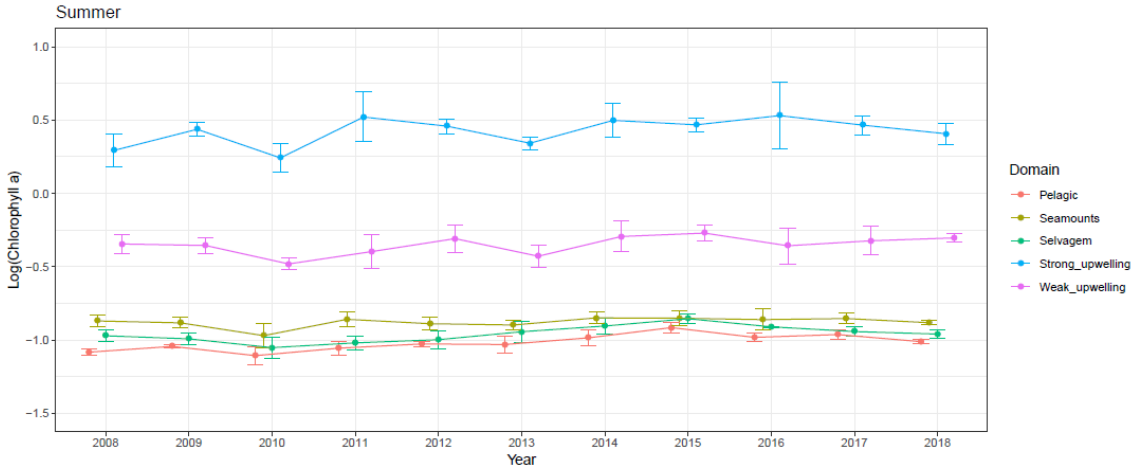
	Winter		Summer	
	Correlation	p-value	Correlation	p-value
Chlorophyll a				
Chub mackerel	-0.29	0.5	-0.05	0.9
Cephalopods	-0.38	0.4	-0.42	0.4
Pilotfish	-.045	0.3	-0.52	0.2
Longspine snipefish	0.67	0.1	0.54	0.2
Sea Surface Temperature				
Chub mackerel	0.14	0.8	0.01	0.9
Cephalopods	-0.15	0.7	0.25	0.6
Pilotfish	-0.09	0.8	-0.08	0.9
Longspine snipefish	-0.21	0.6	0.23	0.6
Wind speed				
Chub mackerel	0.10	0.8	0.14	0.8

Cephalopods	-0.31	0.5	-0.13	0.8
Pilotfish	-0.42	0.3	-0.06	0.9
Longspine snipefish	0.40	0.4	-0.14	0.8
Zonal velocity				
Chub mackerel	-0.39	0.4	-0.18	0.7
Cephalopods	0.22	0.6	-0.17	0.7
Pilotfish	-0.01	0.9	-0.15	0.7
Longspine snipefish	-0.06	0.9	0.28	0.5
Meridional velocity				
Chub mackerel	-0.02	0.9	-0.10	0.8
Cephalopods	0.22	0.6	0.23	0.6
Pilotfish	0.29	0.5	0.12	0.8
Longspine snipefish	-0.38	0.4	0.09	0.9

(a)



(b)



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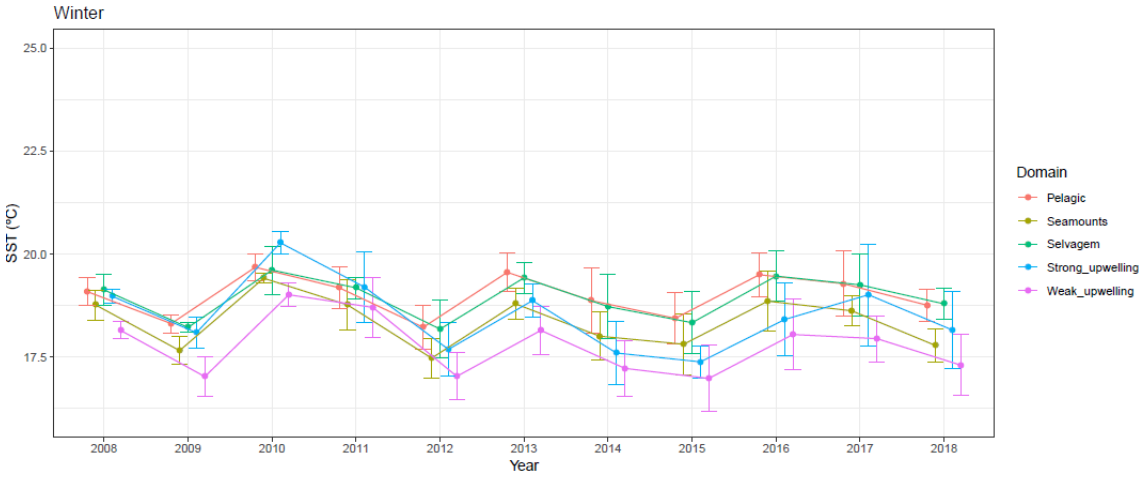
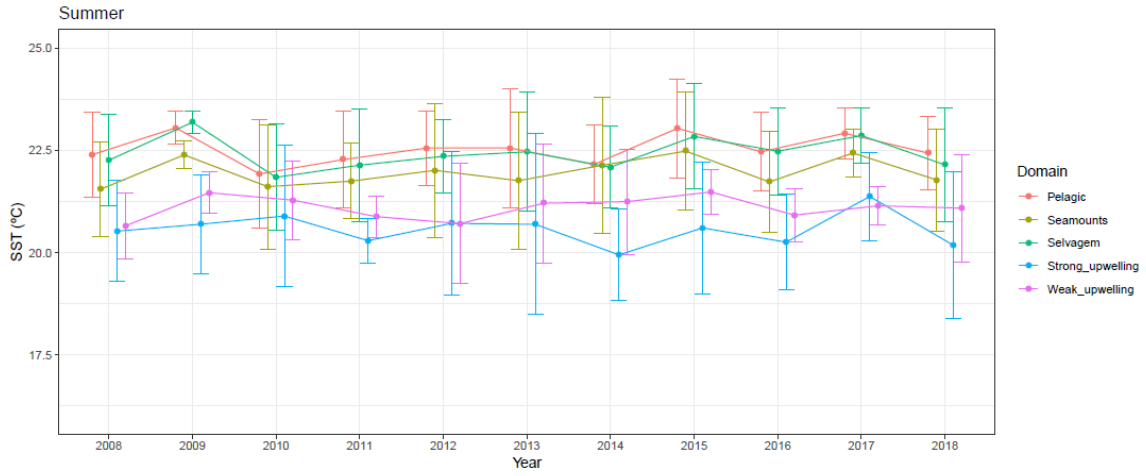
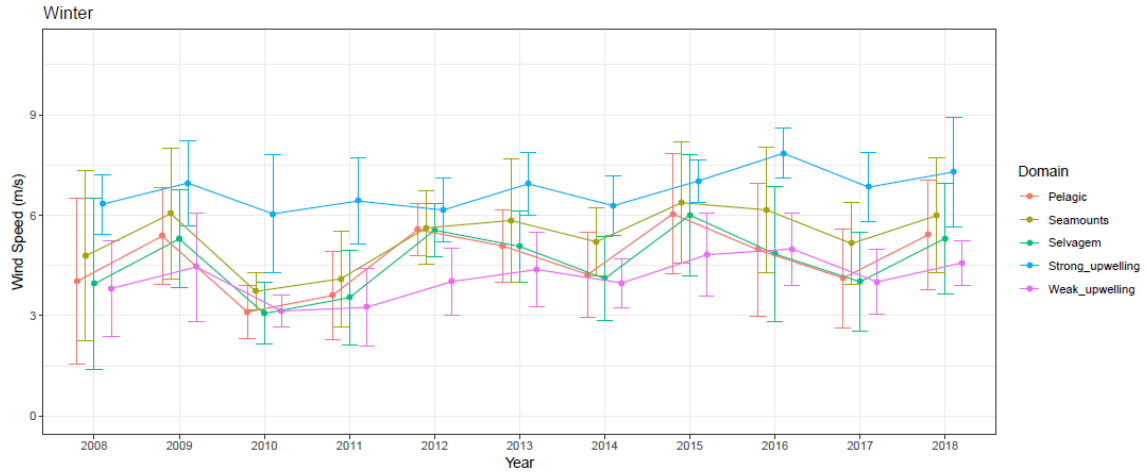

Winter
SST (°C)
25.0
22.5
20.0
17.5
2008
2009
2010
2011
2012
2013
2014
2015
2016
2017
2018
Year
Domain
Pelagic
Seamounts
Selvagem
Strong_upwelling
Weak_upwelling

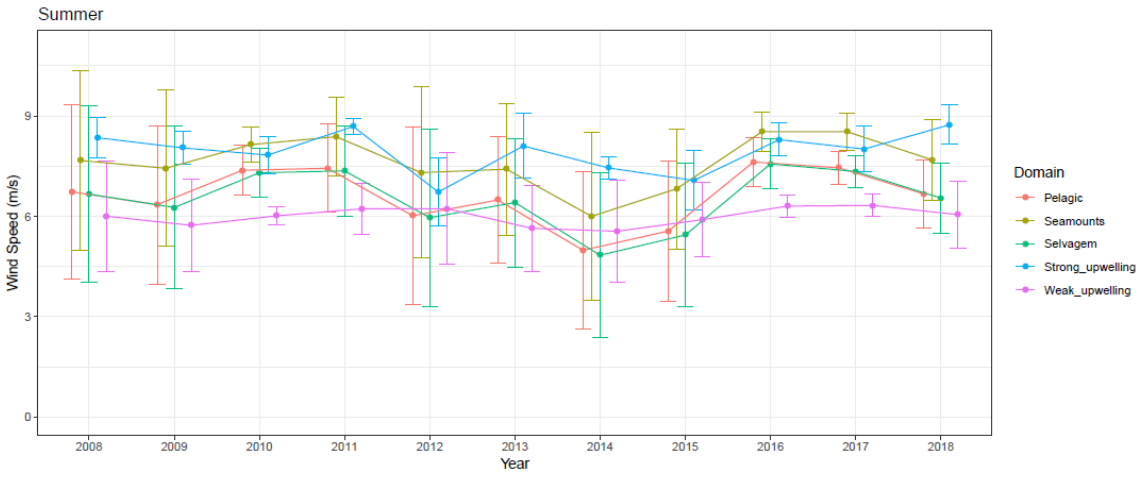
(d)


Summer
SST (°C)
25.0
22.5
20.0
17.5
2008
2009
2010
2011
2012
2013
2014
2015
2016
2017
2018
Year
Domain
Pelagic
Seamounts
Selvagem
Strong_upwelling
Weak_upwelling

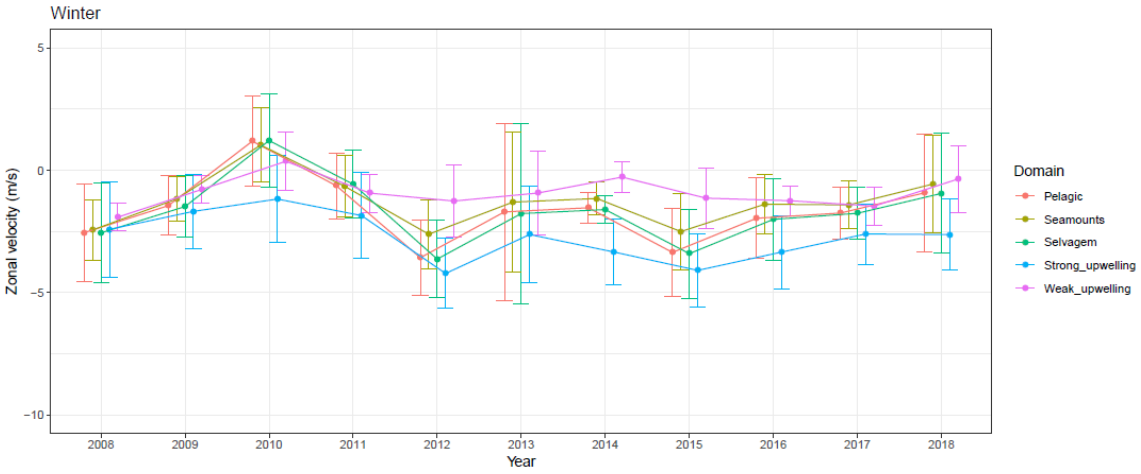
(e)


Winter
Wind Speed (m/s)
9
6
3
0
2008
2009
2010
2011
2012
2013
2014
2015
2016
2017
2018
Year
Domain
Pelagic
Seamounts
Selvagem
Strong_upwelling
Weak_upwelling

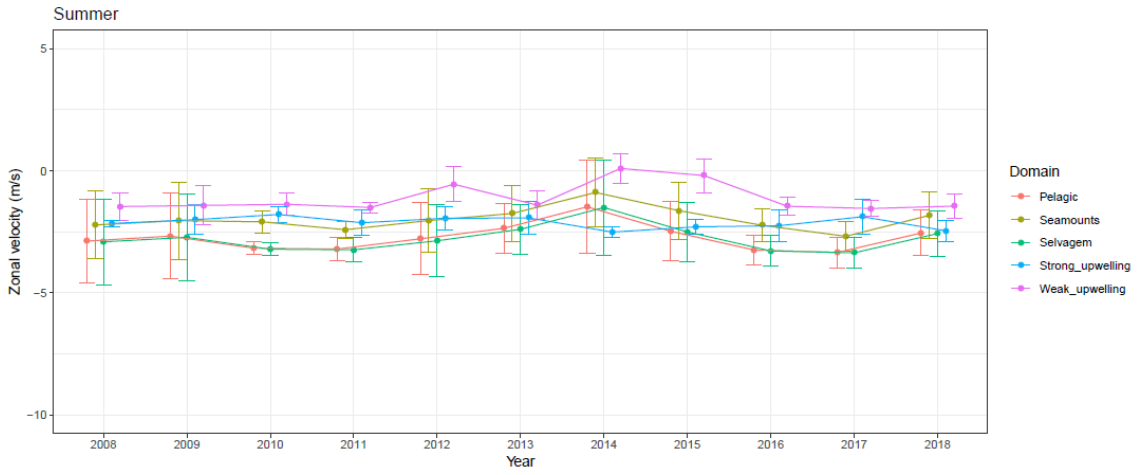
(f)


Summer
Wind Speed (m/s)
9
6
3
0
2008
2009
2010
2011
2012
2013
2014
2015
2016
2017
2018
Year
Domain
Pelagic
Seamounts
Selvagem
Strong_upwelling
Weak_upwelling

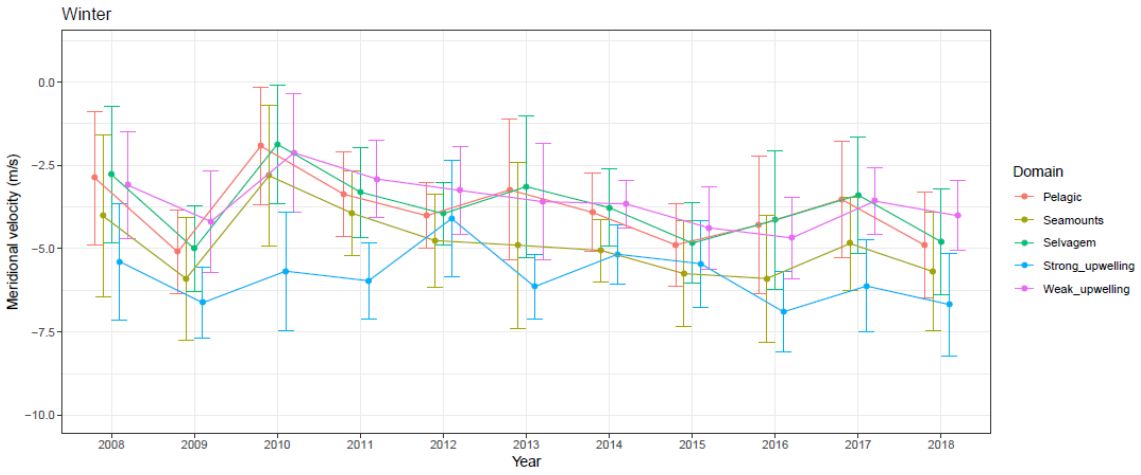
(g)


Winter
Zonal velocity (m/s)
5
0
−5
−10
2008
2009
2010
2011
2012
2013
2014
2015
2016
2017
2018
Year
Domain
Pelagic
Seamounts
Selvagem
Strong_upwelling
Weak_upwelling

(h)


Summer
Zonal velocity (m/s)
5
0
−5
−10
2008
2009
2010
2011
2012
2013
2014
2015
2016
2017
2018
Year
Domain
Pelagic
Seamounts
Selvagem
Strong_upwelling
Weak_upwelling

(i)



(j)

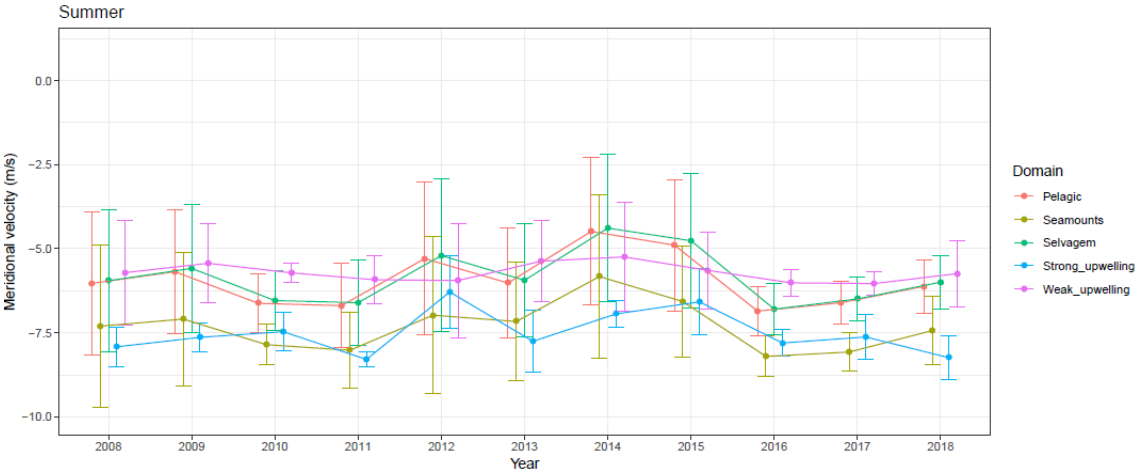


Figure A.2- Interannual variation of oceanographic variables in the 5 domains (Selvagem, Pelagic, Seamounts, SPUR: Strong Permanent Upwelling Region and WPUR: Weak Permanent Upwelling Region). Values correspond to the average values (±SD) of the months from each season (Winter: January-April; Summer: June-September). a) Winter and (b) Summer Chlorophyll a, (c) Winter and (d) Summer Sea Surface Temperature, (e) Winter and (f) Summer Wind speed, (g) Winter and (h) Summer Zonal velocity, and (i) Winter and (j) Summer Meridional velocity.

CHAPTER 6

Credits: Aurore Ponchon

Food web structure of the subtropical oceanic archipelago of Madeira, eastern North Atlantic

Abstract

Oceanic environments, as the surroundings of the archipelago of Madeira, are still in need of base line information on their structure and functioning. This is particularly important in the scope of increasing impacts of fisheries and global changes. In this study, we aim to develop a food web model for the area within the marine Exclusive Economic Zone of the archipelago of Madeira, using the Ecopath with Ecosim software. A total of 57 functional groups were defined, representing both coastal and open ocean areas, and epipelagic and deep-sea realms. The Pedigree index defined the model as having reasonable quality. The total biomass of the Madeira system was calculated as 70 $t \cdot km^{-2}$, with lower trophic levels, like primary producers, zooplankton, other crustaceans and invertebrates, and small pelagic and mesopelagic species, comprising a significant part of its biomass. The food web was characterized by a more linear-like food chain in opposition to a more web-like food chain, with a large proportion of more specialized organisms, like dolphins, shearwaters, and large pelagic fish. Despite the low mean trophic level of the system, the mean trophic level of fisheries was 4.2, targeting mainly top predators, like tunas and Black scabbardfish, which were also the components with most impact in the ecosystem.

Keywords: Top predators, Ecopath with Ecosim, Madeira, Food web, Fisheries

Introduction

The continuous demand for resources has made it increasingly important to understand the ocean as an ecosystem, but such task requires a wealth of information including basic knowledge of its food webs. Food webs are virtual representations of trophic relationships and of the flow of energy and matter through an ecosystem (Cohen et al. 1993). They are useful frameworks to assess the magnitude and importance of trophic relationships with high heuristic value for ecological theories (Link 2002). The study of food webs also allows to depict shifts in the ecosystem, and enables comparisons among similar ecosystems (Cohen et al. 1993). Understanding the structure of food webs and their associated abiotic and biotic factors has far-reaching implications for the conservation of species and their communities, in the sense that the knowledge obtained can be used for management applications (Christensen et al. 2008).

The marine ecosystem has been highly impacted by fisheries in the last 50 to 60 years, when significant examples of technological innovation occurred in larger sized industrial fishing fleets (Valdemarsen 2001), and which continues to deplete stocks at an alarming rate (Worm 2016), despite the warnings and the creation of strategic policies which encourage the implementation of an ecosystem-based approach to fisheries management that would take into account the environmental impacts of fishing, like the European Union Marine Strategy Framework Directive (MSFD; Directive 2008/56/EC, European Parliament 2008). Under sudden environmental and anthropogenic impacts, some species might adapt, while others will tend to migrate to more suitable areas. However, the remainder will eventually disappear, which can further alter the ecosystem functionality and increase the extent of shifts in the community structure and in food webs (Crespo & Dunn 2017, Hillebrand et al. 2018).

In the past decades, the impacts and shifts brought about by global changes and human activities on open oceans have been increasingly noticed. Even though open oceans are often oligotrophic and considered species-poor ecosystems in comparison to coastal areas, they still house complex trophic links of which little is known yet. Studies using stable isotope and fatty acid analysis have been used to describe these food webs (e.g. Bode et al. 2007, Denda et al. 2017, Madgett et al. 2019). However, these are limited to the species sampled and lack power with increasing complexity of the web, as they can carry some uncertainties and errors, like species with multiple organic inputs and consumers which cannot be discerned by one or two stable isotope tracers, or because

isotope ratios are limited and can change according to species composition, metabolic pathway, season or geographic region (Michener & Kaufman 2007).

One way to achieve an ecosystemic view is by means of a mass-balanced model. The Ecopath with Ecosim (EwE) software provides for one of such approaches based on the work of Polovina (1984). The model implemented by EwE considers the biomass and energy flows among different functional groups, and can include fisheries as a particular functional group within the ecosystem (Christensen & Walters 2004). The model has been applied to different aquatic ecosystems (Colléter et al. 2015), focusing on assessment of ecosystem maturity (Chea et al. 2016), temporal variations (Heymans et al. 2004) or impacts of climate change (Tam et al. 2008), fisheries (Torres et al. 2019) or of invasive species (Arias-González et al. 2011).

The archipelago of Madeira is a group of oceanic islands located in the subtropical East Atlantic region, far from the influence of the productive Canary Current Upwelling System. The area comprising this archipelago and that of the Selvagem islands, located ca. 300 km south of the Madeira archipelago, provides a great variety of habitats like intertidal and shelf areas, which represent a small proportion of all habitats, and deep-ocean areas, which are the dominant habitat and with the highest ecological and economic importance (e.g. Hernández & Ortega 2000, Freitas et al. 2012, Farias et al. 2013, Alonso et al. 2018). Madeira, like many other oceanic ecosystems, is characterized by oligotrophic and, therefore, low productivity waters. Still, several predators use these waters, including tunas, seabirds, cetaceans, turtles, small pelagic fish and other deep-sea fish. The fact that there is already a considerable amount of information about the ecology and distribution of many species and groups offer the opportunity to build a mass-balance model for the region, including information about the local fisheries (e.g. Hernández & Ortega 2000, Granadeiro et al. 2006, Alonso et al. 2014, Alves et al. 2015, Gouveia et al. 2019, Raposo et al. 2019). Providing the importance of the oceanic region of Madeira for these top predators, it is important to establish baseline information on the Madeira food web structure. This will allow to depict changes in their biomasses and relationships, but also to model alternative futures according to different predictions on fisheries or global changes.

The aim of this study is to provide a model of the ecosystem of the Exclusive Economic Zone (EEZ) of Madeira using the EwE software. This model synthesises the most recent information available concerning the trophic relationships in the Madeira region, describing the main energy and matter flows among the most important functional

groups of the ecosystem. We also include recent data concerning the prevalence of fisheries in the region and its current impact in the structure of the ecosystem.

Methods

Study Area

This study is focused on the Exclusive Economic Zone (EEZ) of Madeira (hereby referred to as Madeira system), which is an ensemble of groups of islands covering 454,495 km^2, constituted by the archipelago of Madeira, with two main islands (Madeira and Porto Santo) and a group of islands, Desertas, located ca. 20 km to southeast, and the Selvagens islands, at ca. 300 km south of the main group (Figure 1). These volcanic islands are characterized by narrow continental shelves, with the rest of the region being dominated by extensive abyssal plains ca. 4000 m deep. In the north and northeast of Madeira, the abyssal plain is interrupted by the Tore-Madeira Rise, a chain of seamounts ca. 1000 km long and 50 km wide. Seamounts are areas of increased biodiversity (Pitcher et al. 2007) sustained by current-topography interactions, which induces upwelling and enhances primary production (Genin 2004). The Azores Front is the main mesoscale oceanographic feature in the subtropical northeast Atlantic, which allied to the North Atlantic subtropical gyre and the Canary Current, affects primary production, and the depth and intensity of late-winter ocean-mixing in the region (Fründt & Waniek 2012). For these reasons, the corridor created by the Tore-Madeira Rise, the archipelago of Madeira and the Canary Islands, is considered an important fishing area for Portuguese fishing vessels (Campos et al. 2019).

Functional groups and fisheries

The archipelago of Madeira is acknowledged for its biodiversity and fishing tradition. Seabirds, tunas, and many cetaceans are seasonal visitors that use Madeira during the warmer months (Spring to beginning of Autumn). Pelagic forage fish, mainly composed by mackerels and sardines, are prey to these migratory species but also to resident top predators, such as marlins (Istiophoridae) and sharks. Other resident species in these waters include the deep-sea scabbardfish. The vast deep waters surrounding Madeira island harbour two species, the Black scabbardfish *Aphanopus carbo* and Intermediate scabbardfish *A. intermedius*, which together contributed with the highest proportion of total landings in the archipelago between 2000-2013 (Hermida & Delgado 2016). However, since then, the landings of tunas have dominated the fisheries in Madeira again, as it was before 2000 (Gouveia et al. 2017). The tuna pole-and-line fishery is only

present between March and November (Gouveia & Mejuto 2003), but it is the most important revenue for fishermen in Madeira, mainly targeting Bigeye tuna *Thunnus obesus* and Skipjack tuna *Katsuwonus pelamis* (Hermida & Delgado 2016). Purse seining is the third most important type of fishery in Madeira in terms of catch and economic value, and targets small pelagic fishes, like Blue jack mackerel *Trachurus picturatus*, Atlantic chub mackerel *Scomber colias*, and to a lesser extent European pilchard *Sardina pilchardus*. Small fisheries are also reported in Madeira but have less economic importance and represent very low catches. These include the bottom longline and handline and recreational fisheries, which also target top predators, like large pelagic species and squids (Hermida & Delgado 2016). Overall, the Madeira fleet is dominated by artisanal fishing vessels.

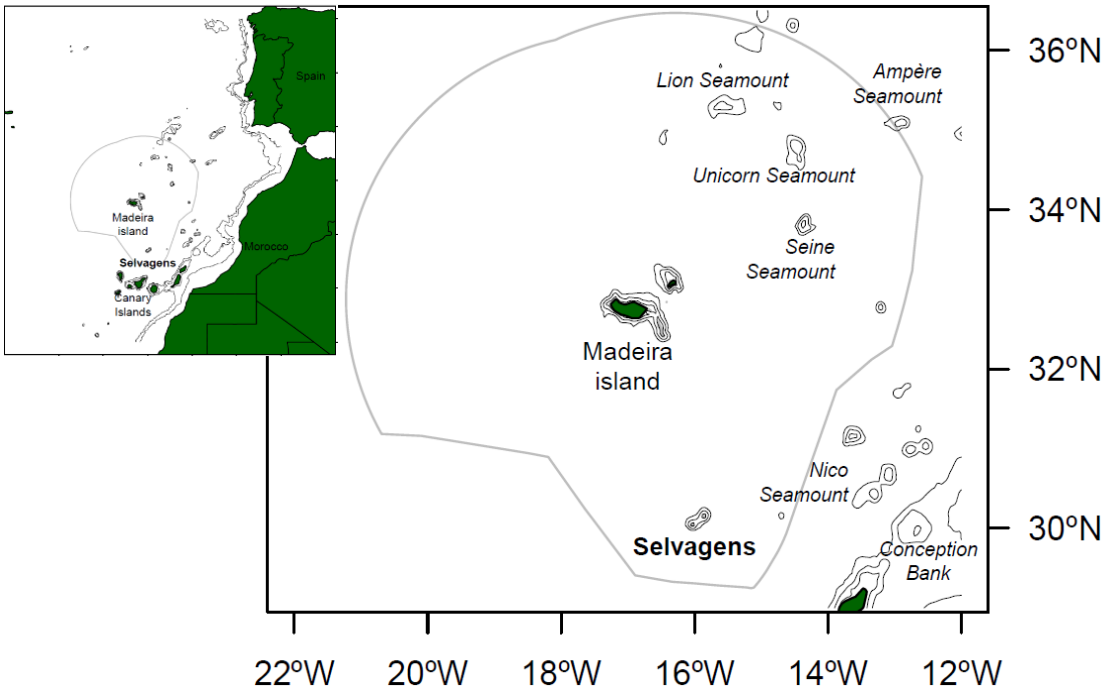


Figure 2 - Exclusive Economic Zone (EEZ) of the archipelago of Madeira (grey line), the study area. Bathymetric lines correspond to 200, 1000 and 2000m.

Modelling Approach

The food web model presented in this study was constructed using the EwE software version 6.6.3 (www.ecopath.org). This software is a food web modelling facility that provides a trophic steady mass-balanced snapshot of the ecosystem (Ecopath), but can also create temporal dynamics (Ecosim) resulting from time varying biomass and/or

harvest rates (Christensen et al. 2008). In this study, we will use the Ecopath facility alone.

There are two master equations in the parameterization of EwE. The first describes the production term and ensures a mass balance between groups by exploring the energy transfer in each functional group so the inputs will equal the outputs:

$$B_i(P/B)_i EE_i - \sum_{j=1}^{n} B_j(Q/B)_i DC_{ji} - Y_i - BA_i - E_i = 0 \quad (1)$$

Where B_i is the mean biomass of the functional group i (in $t \cdot km^{-2}$); P/B_i is the production/biomass ratio of the functional group i ($year^{-1}$); EE_i is the fraction of the functional group i consumed by a predator or caught in fisheries (i.e., the proportion of the production that is used in the system, designated as Ecotrophic Efficiency); Q/B_i is the food consumption per biomass unit of the functional group i ($year^{-1}$); DC_{ij} is the fraction of the functional group i consumed by predator j; Y_i is the total fishery catch rate of the functional group i ($t \cdot km^{-2}$); E_i is the net migration rate of the functional group i ($year^{-1}$); and BA_i is the biomass accumulation rate for the functional group i ($year^{-1}$).

The second equation is based on the principle of conservation of matter and describes the energy balance for each functional group:

$$Q = P + R + UAF \quad (2)$$

Where Q is the consumption of a functional group (in $t \cdot km^{-2} \cdot year^{-1}$), P is the sum of production of the same group ($t \cdot km^{-2} \cdot year^{-1}$), R is its respiration, and UAF is the unassimilated food by that group.

Ecopath can estimate missing parameters and ensure the energy balance within the different functional groups by using the links between the production of each functional group and the consumption of all functional groups (Christensen et al. 2008). The software includes routines which consider the estimation uncertainty (generally designated as pedigree) associated with the model inputs of four parameters: biomass, production/biomass and consumption/biomass ratios, and ecotrophic efficiency of the different functional groups (Christensen & Walters 2004, Plaganyi 2007). At least three of these parameters need to be provided to the model so it can estimate the missing parameter. Additional information on diet composition and fisheries is also needed to complete the model (Christensen & Walters 2004).

Model Structure and Parameterization

The present model represents the food web of the EEZ of the archipelago of Madeira, including the vertical layers and from coastal to pelagic domains of this ecosystem.

The species included in this model comprised the most common and best documented species for the EEZ of Madeira, including those that are targeted by commercial fisheries (Hermida & Delgado 2016). Whenever data on biomass, production, consumption, and diet of relevant species were not available for the region, we resorted to the information available for similar ecosystems, preferably in the east Atlantic region. These species were grouped according to their diet and feeding ecology, and primary producers of the ecosystem, in 56 functional groups, representing seabirds (3 groups), marine mammals (6), sea turtles (1), fish (32), cephalopods (3), other invertebrates (6), algae (1), and plankton (4) (see Supplementary Materials, Table S1). The detritus was also included in this list. Some groups composed of one or several species were specifically defined considering their economic importance in the region. Other groups were split into different size classes, whether because good quality data were available for these groups or because predator dietary data was fine enough to justify prey-size stratification.

Due to their economic and social importance, Black scabbardfish (including both *Aphanopus carbo* and *A. intermedius*), Bigeye tuna, Skipjack tuna *Katsuwonus pelamis*, Atlantic chub mackerel *Scomber colias* and Blue jack mackerel *Trachurus picturatus*, were included as individual functional groups. The Sperm whale *Physeter macrocephalus* and the Monk seal *Monachus monachus* were also separated into single species functional groups due to their particular ecology and behaviour, more specifically due to the use of deep waters and coastal areas, respectively. Multi species groups were arranged according to biological and ecological traits, such as diet (herbivores, carnivores), domain (epipelagic, mesopelagic, demersal) or size (see Supplementary Materials, Table S1).

Biomass data for many groups was not available for our study region and was therefore estimated by the model. In the remaining cases (23%), ecotrophic efficiency was the parameter to be estimated by the model. Whenever possible, parameters P/B, Q/B or P/Q were either based on recent and local literature (e.g. Morissette et al. 2010, Alves et al. 2018) or obtained from models of similar oceanographic and ecological areas (e.g. Morato et al. 2016). We also used data on production and consumption from studies elsewhere in the Atlantic (e.g. Piroddi et al. 2015), whenever possible, and on information on lengths and growth coefficients available in Fishbase (Froese & Pauly 2020) to

calculate natural mortality. A similar approach was applied to diet composition data. For further information on the input parameters used in the model, see Supplementary material, Table S1 and Table S2. The period of 2005-2010 was chosen as reference to build the model as most data was originated from those years.

Fisheries data from Madeira were obtained from Direção Regional de Estatística da Madeira (DREM; estatistica.madeira.gov.pt), Instituto Nacional de Estatística (INE; www.ine.pt), and local studies (e.g. Gouveia et al. 2019). Currently, there are six gear types in Madeira, purse seining (small pelagic fish), handline and pole-line fishing (large pelagic fish, tuna, demersal fish), drifting longlines (deepwater species, scabbardfish), set or bottom longlines (finfish, demersal fish), fishing pots and traps (finfish, various demersal fish, crustaceans and cephalopods), and game fishing (marlin) (DGPA 2010, Vallerani et al. 2017). Catch values were estimated based on a dataset of 17 years (2000-2017; see Supplementary material, Table S3). Discard values were estimated based on studies carried out in the Madeira region (Martins & Ferreira 1995, Severino 2004) and studies from the Canary Islands (Pajuelo et al. 2010).

Ecopath incorporates a tool to describe the origin and quality of the data input to the model, enabling an informal assessment of the reliability of the model. The Pedigree index is attributed to each input parameter and each functional group, varying between 0 and 1, with lower values representing non-local and highly uncertain data, such as estimations by the model, and higher values representing local and precise data (Christensen & Walters 2004). The final index can vary between 0 and 1, indicating a poor or high-quality final model, respectively.

Model outputs

The model provides the (average) Trophic Level (TL) of each functional group based on the diet composition of all groups, and the Omnivory index (OI), which is defined by the degree of trophic specialization of each consumer (Christensen et al. 2008). The Connectance index describes whether the food web is web or linear-like by measuring the number of food links in a system in relation to the total number of possible links (Gardner & Ashby 1970). The System Omnivory Index (SOI) is defined by the average Omnivory index of all consumers weighted by the logarithm of their consumption, which can indicate the trophic specialization of the whole system. Diet overlap was estimated according to the similarities in the diet among different functional groups in the model, following Pianka's (1974) equation.

To assess the most important and impacting/impacted functional groups in the Madeira ecosystem, we used the Keystoneness index and the Mixed trophic impact (MTI) routine, respectively. The Keystonenness index identifies the species that have large impacts on other species or functional groups, despite their relative low abundances (Paine 1995, Libralato et al. 2006). The MTI also enables the assessment of the impact of fisheries in each functional group and in the food web.

Results

Model balancing and Parameters of the balanced model

The Pedigree index for the Madeira System was estimated at 0.39 (Table 1). Final input parameters of each functional group used for the Madeira ecosystem model are described in Table 2. Ecotrophic efficiency values varied greatly according to the proportion of the production of each functional group used by the system. The lowest values corresponded to marine mammals, seabirds and pelagic sharks, while intermediate trophic levels and other functional groups targeted by fisheries presented the highest values.

Table 1 – Summary statistics and ecosystem attributes of the Madeira system

Parameter	Value	Units
Ecosystem properties		
Sum of all consumption	1066.338	$t \cdot km^{-2} \cdot y^{-1}$
Sum of all exports	755.208	$t \cdot km^{-2} \cdot y^{-1}$
Sum of all respiratory flows	570.879	$t \cdot km^{-2} \cdot y^{-1}$
Sum of all flows into detritus	1141.623	$t \cdot km^{-2} \cdot y^{-1}$
Sum of all production	1608.277	$t \cdot km^{-2} \cdot y^{-1}$
Total system throughput (TST)	3534.049	$t \cdot km^{-2} \cdot y^{-1}$
Total net primary production	1326.086	$t \cdot km^{-2} \cdot y^{-1}$
Net system production	755.207	$t \cdot km^{-2} \cdot y^{-1}$
Total biomass (excluding detritus)	70.747	$t \cdot km^{-2} \cdot y^{-1}$
Ecosystem maturity		
Total primary production/total respiration	2.323	
Total primary production/total biomass	18.744	
Total biomass/total throughput	0.020	
Food web structure		
Mean Transfer Efficiency	15.102	%
Connectance Index	0.135	
System Omnivory Index	0.232	
Model reliability		
Pedigree index	0.39	

Summary statistics

The summary statistics and flow indices are presented in Table 1. The model estimated a total biomass (excluding detritus) of 70.75 $t \cdot km^{-2}$, of which 22.8% were primary producers and 26% were zooplanktonic species. Invertebrates were by far the group with the highest biomass (36.8%), of which molluscs and other benthos constituted the major proportion. Cephalopods, crabs and shrimps are also accounted in this group. Fish followed with 14.2% of all biomass. Air-breathing fauna, such as seabirds, marine mammals and sea turtles only represented 0.15% of the biomass found in this ecosystem.

Trophic levels

The food web structure, interactions and flow diagram of the Madeira ecosystem is represented in Figure 2. The Madeira ecosystem model was composed by five trophic levels (TL), with an average TL (biomass-weight average) of 2.19±0.79 (Table 2). The maximum trophic level was 5.03 (Sperm whale). The deep-sea sharks and Killer whale followed with TL=4.69, pelagic sharks with TL=4.57 and the Black scabbardfish with TL=4.56. Other functional groups with a TL> 4 included species of large pelagic fish, marine mammals, seabirds, tunas, and cephalopods. Small pelagic and mesopelagic fish had TL between 2.86 and 3.36, and TL between 2.96 and 3.08, respectively. Baleen whales, coastal birds, small petrels and sea turtles had TLs between 3.72 and 3.98.

Predation and Omnivory index

Excluding detritus and primary producers, zooplanktonic species were the most consumed functional groups in the Madeira system, both in number of predators (29) and average proportion in the diet of all predators of the ecosystem (19%; see Supplementary materials, Table S4). Myctophids and small mesopelagic followed with the next higher number of predators (26 and 16). Small pelagic fishes (including Chub mackerel and Blue jack mackerel) had an average proportion in the diet of predators similar to mesopelagic fish (10% and 9%, respectively). Small/medium mesopelagic cephalopods and shrimps were also among the functional groups with the highest number of predators (21 and 20, respectively) and with a higher average proportion in the diet of predators (5% and 3%, respectively; see Supplementary materials, Table S4).

Among top predators, dolphins, shearwaters, tunas, and large pelagic fish had the most similar diet when analysing the resolution used in this model. Toothed whales and Sperm whales also fed on similar prey.

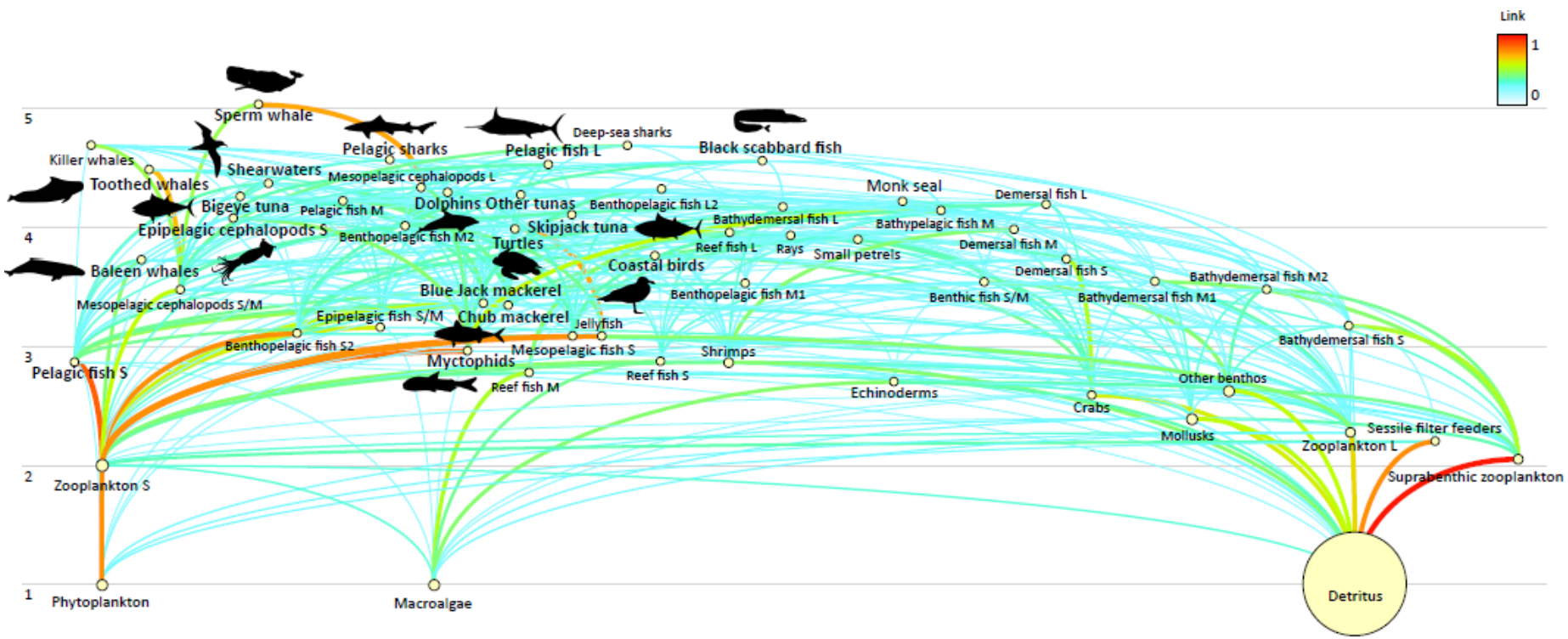


Figure 2 – Ecopath flow diagram representing the food web structure and trophic levels of the Madeira system. The different sizes of the circles represent the logarithmic biomass of each functional group. The colour of each link corresponds to the proportion of the functional group on the diet of its consumer; light blue corresponds to proportions close to 0 and red to proportions close to 100%.

Overall, omnivory index values were low, with the maximum value reaching 0.55 for medium reef-associated fish (Table 2). Chub mackerel followed with the next highest value. The index among top predators varied between 0.07 for turtles and 0.39 for Monk seal (Table 2).

Mixed Trophic Impact and Keystoneness index

Detritus, macroalgae, phytoplankton, small-sized zooplankton and small pelagic fish had the highest averaged positive impacts on other species (see Supplementary materials, Figure S1). On the other hand, baleen whales, dolphins, and medium bathypelagic fish (>1000m) were the functional groups with the highest averaged negative impacts. The model also identified top predators, like dolphins, large demersal fish, Killer whales, and pelagic sharks as keystone groups in the Madeira ecosystem (see Supplementary materials, Table S3).

Fisheries

The average total catches in Madeira system between 2000-2017 was 0.019 $t \cdot km^{-2}$, targeting a mean trophic level of 4.26, and with a gross efficiency of the fishery at 0.000015.

Tunas and other large pelagic fish presented the highest mortality rate by fisheries (F/Z >90%), followed by Black scabbardfish (67%), and medium pelagic fish (46%; Table 2).

Table 2 - Input and output parameters of the Madeira Ecosystem model. Estimated values by Ecopath are in bold. P: Production ($t \cdot km^{-2} \cdot yr^{-1}$); B: Biomass; Q: Consumption ($t \cdot km^{-2} \cdot yr^{-1}$); EE: Ecotrophic efficiency; F: Fishing mortality; Z or P/B: Total mortality; OI: Omnivory Index. * fished species

Group name	Trophic level	Habitat (%)	Biomass ($t \cdot km^{-2}$)	P/B (yr^{-1})	Q/B (yr^{-1})	EE	P/Q (yr^{-1})	F/Z	OI
Baleen whales	3.72	100	0.0409	0.01	6.26	**0.00**	**0.0016**		**0.36**
Toothed whales	4.48	100	0.0039	0.04	9.92	**0.27**	**0.0040**		**0.14**
Sperm whale	5.03	100	0.0555	0.05	5.03	**0.00**	**0.0099**		**0.17**
Killer whales	4.69	100	0.0001	0.02	7.76	**0.00**	**0.0026**		**0.20**
Dolphins	4.29	100	0.0086	0.05	13.74	**0.26**	**0.0036**		**0.11**
Monk seal	4.22	1	$2.0 \cdot 10^{-7}$	0.08	13.15	**0.00**	**0.0061**		**0.40**
Shearwaters	4.37	100	0.0001	0.09	42.72	**0.00**	**0.0021**		**0.17**
Small petrels	3.90	100	$3.5 \cdot 10^{-5}$	0.19	91.24	**0.42**	**0.0021**		**0.29**
Coastal birds	3.76	15	$4.1 \cdot 10^{-6}$	0.05	69.73	**0.00**	**0.0007**		**0.10**
Turtles	3.98	100	0.0005	0.15	3.50	**0.93**	**0.0429**	**0.1530**	**0.07**
Pelagic sharks	4.57	100	**0.0005**	0.27	1.44	0.40	**0.1875**	**0.4000**	**0.30**
Deep-sea sharks*	4.69	95	**0.0387**	0.36	2.01	0.60	**0.1791**	**0.0417**	**0.30**

Rays	3.93	90	**0.0004**	0.22	2.29	0.60	**0.0961**		**0.22**
Pelagic L*	4.53	100	**0.0002**	0.73	5.27	0.95	**0.1385**	**0.9500**	**0.15**
Bigeye tuna*	4.26	100	**0.0016**	1.88	6.00	0.95	**0.3133**	**0.9208**	**0.18**
Skipjack tuna*	4.10	100	**0.0027**	1.43	10.40	0.95	**0.1375**	**0.9163**	**0.27**
Other tunas*	4.27	100	**0.0003**	0.96	8.07	0.95	**0.1190**	**0.9500**	**0.23**
Pelagic M*	4.22	100	**0.0001**	0.87	3.93	0.95	**0.2214**	**0.4613**	**0.05**
Epipelagic S/M	3.16	100	**0.0124**	0.83	5.35	0.95	**0.1551**		**0.53**
Pelagic S*	2.86	100	**0.1102**	1.98	16.03	0.95	**0.1235**	**0.0002**	**0.38**
Chub mackerel*	3.34	100	**0.0293**	1.98	5.60	0.95	**0.3536**	**0.0163**	**0.14**
Blue Jack mackerel*	3.36	100	**0.0317**	1.76	6.50	0.95	**0.2708**	**0.0257**	**0.27**
Reef-associated L	3.95	15	**$4.0 \cdot 10^{-7}$**	0.44	3.42	0.95	**0.1287**		**0.12**
Reef-associated M*	2.78	15	**0.0008**	1.26	12.14	0.95	**0.1038**	**0.0040**	**0.55**
Reef-associated S	2.87	15	**0.0081**	2.49	17.53	0.95	**0.1420**		**0.47**
Demersal L*	4.19	30	**0.0056**	0.57	2.88	0.95	**0.1979**	**0.0243**	**0.28**
Demersal M*	3.98	30	**0.0050**	0.34	3.67	0.95	**0.0926**	**0.0026**	**0.06**
Demersal S*	3.73	30	**0.0101**	1.23	6.30	0.95	**0.1952**	**0.0013**	**0.28**
Benthic S/M	3.54	30	**0.0078**	1.08	5.87	0.95	**0.1840**		**0.17**
Mesopelagic S	3.08	100	**1.1647**	2.27	14.34	0.95	**0.1583**		**0.15**
Myctophids	2.96	100	**2.9788**	1.76	13.88	0.95	**0.1268**		**0.23**
Benthopelagic L*	4.32	100	**0.0020**	0.57	2.04	0.95	**0.2794**	**0.0558**	**0.26**
Benthopelagic M1*	3.53	50	**0.0112**	1.01	4.29	0.95	**0.2354**	**0.0053**	**0.38**
Benthopelagic M2*	4.01	100	**0.1949**	0.30	3.28	0.95	**0.0915**	**0.0003**	**0.04**
Benthopelagic S	3.11	100	**0.1381**	1.20	5.52	0.95	**0.2174**		**0.14**
Bathypelagic M	4.14	100	**1.8069**	0.56	4.46	0.95	**0.1256**	**$7.1 \cdot 10^{-5}$**	**0.13**
Bathydemersal L*	4.17	30	**0.0164**	0.42	2.98	0.95	**0.1409**	**0.0036**	**0.35**
Bathydemersal M1	3.54	30	**0.1697**	0.30	2.23	0.95	**0.1345**	**$2.7 \cdot 10^{-5}$**	**0.20**
Bathydemersal M2	3.48	90	**1.5556**	0.35	2.42	0.95	**0.1446**	**0.0001**	**0.12**
Bathydemersal S	3.17	90	**1.6837**	0.70	5.91	0.95	**0.1184**		**0.13**
Black scabbard fish*	4.56	30	**0.0259**	0.53	2.52	0.95	**0.2103**	**0.6667**	**0.29**
Epipelagic cephalopods S*	4.07	100	**0.0147**	8.50	25.00	0.95	**0.3400**	**$1.7 \cdot 10^{-5}$**	**0.21**
Mesopelagic cephalopods L	4.33	100	**0.0824**	2.50	10.00	0.95	**0.2500**		**0.29**
Mesopelagic cephalopods S/M	3.47	100	**0.3267**	4.45	16.86	0.95	**0.2639**		**0.14**
Jellyfish	3.08	100	**0.0265**	13.87	50.48	0.95	**0.2748**		**0.44**
Crabs	2.59	100	**0.1792**	1.60	10.00	0.95	**0.1600**		**0.37**
Shrimps	2.86	100	**3.6210**	1.45	11.74	0.95	**0.1235**		**0.51**
Echinoderms	2.70	100	**1.5917**	1.72	6.91	0.85	**0.2489**		**0.05**
Molluscs	2.39	100	**8.7528**	2.24	5.50	0.90	**0.4073**		**0.30**
Other benthos	2.63	100	**8.6220**	2.74	12.25	0.90	**0.2237**		**0.42**
Sessile filter feeders	2.20	100	**2.8427**	0.80	9.00	0.50	**0.0889**		**0.02**
Suprabenthic zooplankton	2.05	100	**3.7398**	16.00	42.00	0.95	**0.3810**		**0.16**
Zooplankton L	2.28	100	**3.7805**	8.70	29.00	0.95	**0.3000**		**0.24**
Zooplankton S	2.00	100	10.9000	11.21	43.29	**0.69**	**0.2590**		**0**
Macroalgae	1.00	10	**6.8237**	27.95		0.50			**0**
Phytoplankton	1.00	100	9.3200	121.82		**0.31**			**0**
Detritus	1.00	100	1000			**0.34**			**0**

Discussion

This study represents a snapshot of the ecosystem state of Madeira system in 2005-2010 and constitutes the first mass-balance model for this region. The lower trophic levels (primary producers, zooplankton, crabs and shrimps, benthic invertebrates and sessile filter-feeders, and small pelagic and mesopelagic fish) represented the highest proportion of biomass in this ecosystem, and also the most predated groups. The structure of the food web is characterized by a more linear-like food chain in opposition to a web-like food chain, with a high proportion of specialists, like dolphins and other epipelagic feeders. Some of these top predators were also considered keystone species, i.e. with high impact on the structure and functioning of the ecosystem. Fisheries showed to have significant impacts on top predators, like tunas and Black scabbardfish.

Balancing of the model

The large variety of functional groups defined aimed at including the highest number of species from which we could find appropriate information, belonging to all vertical layers and distances to the coast. Like in many other regions (e.g. Couce-Montero et al. 2015, Morato et al. 2016, Veiga-Malta et al. 2019), despite the existence of local and good quality data for most groups, many input parameters still had to be taken from studies from nearby regions, other models or, ultimately, estimated by the model. The Pedigree index estimated a value of 0.39 which is lower than the average calculated by Colléter et al. (2015), 0.472 (n=34 models), but in the upper range of the intermediate pedigree (0.200-0.399), as considered by Morissette (2007), who assessed the quality of a set of 50 models. Even so, we are aware of the necessity of refining the information provided for some of the parameters of the model, in order to improve the quality of the model.

Ecosystem structure

The total biomass estimated by the model, 70.75 $t \cdot km^{-2}$, was similar to the Gulf of Cadiz (80.02 $t \cdot km^{-2}$; Torres et al. 2013), but higher than for the Azores EEZ system (24.73 $t \cdot km^{-2}$; Morato et al. 2016) and lower than that for the Portuguese shelf (116 $t \cdot km^{-2}$; Veiga-Malta et al. 2019). The higher biomass values are most probably due to the influence of upwelling processes in the Portuguese coastal shelf, which enhance biological productivity and provide conditions to support higher abundances of organisms. The Madeira system is dominated by lower trophic levels in terms of total biomass, like benthonic invertebrates and sessile filter feeders, primary producers, and

zooplankton. Fish only corresponded to 14% of all biomass, cephalopods corresponded to 0.5%, and air-breeding species only to 0.15%. This type of composition was also observed in other oceanic ecosystems in the same region, the Gran Canaria and the Azores EEZ systems (Couce-Montero et al. 2015, Morato et al. 2016), but differed from coastal systems, where fish represented the highest proportion of biomass (Torres et al. 2019, Veiga-Malta et al. 2019, Paradell et al. 2020).

The structure of a food web can be characterized by a more linear or more web-like food chains, depending on the number of links of each species, i.e. depending on the overall diet specialization. This can be assessed by two indexes estimated by the model, the System Omnivory Index (SOI) and the Connectance Index (CI). The Madeira system showed a more linear food web pattern (SOI=0.23 and CI=0.13), with relatively more specialists than generalists (the Omnivory Index varied between 0.01-0.54), which agrees with the low complexity of the food web. The Atlantic chub mackerel, an opportunistic species with a varied diet of planktonic and fish species in Madeira (Romero et al. submitted - Chapter 2), had among the highest omnivory indexes in the ecosystem, 0.53. On the other hand, dolphins, turtles, shearwaters, tunas, and large pelagic fish presented a low omnivory index (<0.2), showing a highly specialized diet composed of few small epipelagic species. These indexes presented comparable values to other nearby systems, in which similar taxonomic resolutions were used, both oceanic (Morato et al. 2016) and coastal (Heymans et al. 2004, Essekhyr et al. 2019, Torres et al. 2019, Veiga-Malta et al. 2019), and also to the average values estimated for the east Atlantic (Heymans et al. 2014).

Zooplanktonic species, myctophids, other small mesopelagic and epipelagic fish as well as cephalopods are the most predated species in this ecosystem. The MTI analysis has further indicated them as having high positive impacts on the other functional groups, since they are the main prey of many predators. Yet, some top predators (dolphins, Killer whales, pelagic sharks, and large demersal fish) also had important impacts on the biomass of several species and in the ecosystem, overall, as the MTI and Keystoneness index suggested. Despite their overall low biomass, these groups were composed by animals with high nutrition needs and, therefore, with high use of marine resources. Thus, top predators have a strong influence on ecosystem dynamics and on the abundance of other species, maintaining the community organization and biodiversity (Mills et al. 1993, Paine 1995). Dolphins, shearwaters, tunas, and other large pelagic fish had among the higher prey overlap between functional groups. These are epipelagic consumers in the

oceanic waters of Madeira, feeding mainly of mackerels and other small pelagic fish, on cephalopods, and few small mesopelagic fish (Veiga et al. 2011, Alonso et al. 2014, Dromby 2018, Romero et al. submitted - Chapter 3 and 5). Even the Bigeye tuna, which is majorly mesopelagic elsewhere (Ohshimo et al. 2018, da Silva et al. 2019), is mostly an epipelagic feeder in Madeira (Romero et al. Submitted - Chapter 3). Toothed and Sperm whales occupy a different niche, feeding mostly on mesopelagic species, like cephalopod and myctophids (Clarke et al. 1993, Dromby 2018). Such information is valuable because it gives an overview of the most impacting and impacted species and on possible shifts in the food web in the face of continued fishing or global changes.

Overall, the TLs of several functional groups for the Madeira system were similar to the ones defined in other models in nearby regions, like the Gran Canaria system (Couce-Montero et al. 2015), the Azores EEZ (Morato et al. 2016), and the Portuguese shelf systems (Torres et al. 2019, Veiga-Malta et al. 2019). Unfortunately, the diet of many deep-sea species from the northeast Atlantic is not well studied, which led to differences in the estimation of the TL. Further studies on the diet of these groups are needed to obtain a better model of the food web structure in the ecosystem of Madeira.

Fisheries

In Madeira, fisheries target mostly top predators, like tunas and scabbardfish (Hermida & Delgado 2016), which are common in oceanic regions like the Azores (Morato et al. 2016). This is why the average trophic level of fisheries in Madeira is so high, even higher than in the Azores (3.95; Morato et al. 2016). In Madeira, fisheries of intermediate forage fish are less developed than in coastal areas due to their low profitability in terms of cost/efficiency of the fisheries and cost at the market (Hermida & Delgado 2016). The total fisheries catch for the Madeira system is expected to be low (0.019 $t \cdot km^{-2}$) due to the low ratio of fishing areas in relation to the study area. This estimation is similar to the catches observed in the Azores EEZ where a similar study area is analysed (0.02 $t \cdot km^{-2}$; Morato et al. 2016), but lower than the values observed in coastal systems (e.g. Torres et al. 2019, Veiga-Malta et al. 2019, Paradell et al. 2020), which present high productivity and biomasses, but also smaller study areas. Consequently, the gross efficiency of fisheries in Madeira system also had lower estimations than systems with higher catches (e.g. Couce-Montero et al. 2015, Veiga-Malta et al. 2019).

Fisheries were the most important factor of mortality of tunas and other large pelagic fish, and of Black scabbardfish in the oceanic region of the archipelago of

Madeira. However, our model suggested that the ecosystem should remain in equilibrium if fisheries are to continue exploiting the marine resources of Madeira at the same rate. While this might be true in the case of the Black scabbardfish, as its spawning grounds are in the region of Madeira (Farias et al. 2013), for tunas, which are migratory species, the health of the population will mostly depend on its status in the spawning and nursing areas. Nevertheless, while the Skipjack tuna population status remains unknown, the Atlantic Bigeye tuna stock has been considered overexploited by ICCAT (2018), which may raise concerns on the sustainability of this fisheries. A steep reduction in the stock of any of these three groups of species will have significant impacts on the structure of the food web, most probably impacting the epipelagic and deep-sea ecosystems, and consequently also impacting the economy of the archipelago of Madeira.

Conclusion

As done in models from other ecosystems (e.g. Vasconcellos & Watson 2004), we attempted to build a comprehensive representation of the Madeira system, putting together the highest possible number of representative groups. However, for some there was less regional information available, such as for deep-sea species and lower trophic levels (plankton, crustaceans). These gaps were filled by data from other similar regions, which probably resulted in a relatively low Pedigree Index and, thus, lower suitability and quality of the model. To correct this, it will be important to estimate the biomass of the most important species in the Madeira system but also study the diet and reproduction of these groups, to raise the confidence of the model.

This study is a first effort to build a model of the food web structure of Madeira and a step forward towards the understanding of this ecosystem. It has also given us valuable insights on the most important trophic levels, on the interactions among species, and a brief look at some of the impacts that fisheries may have over the marine ecosystem of Madeira. A more refined version of this model will not only allow to create a well-sustained ecosystem-based fishery management but will also allow to predict possible outcomes of different fisheries scenarios, and even of global changes, providing the opportunity to define the most adequate strategies towards a more sustainable marine resource exploitation.

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Supplementary Materials

Table S4 - Input data and references used for each functional group for the Madeira EEZ ecosystem model. S – Small, M – Medium, L – Large

1. Baleen whales (*Balaenoptera borealis, Balaenoptera brydei, Balaenoptera physalus*)		
Biomass	0.040888 $t \cdot km^{-2}$	Density estimates based on boat surveys (Freitas et al. 2014) Individual body weight (Aguilar 2009, Horwood 2009, Kato & Perrin 2009)
P/B	0.01 $year^{-1}$	Morissette et al. 2010
Q/B	6.26 $year^{-1}$	Morissette et al. 2010
EE	Estimated by the model	
Diet		Kawamura 1980, Tershy et al. 1993, Konishi et al. 2009
2. Toothed whales (*Globicephala macrorhynchus, Grampus griseus, Kogia breviceps, Mesoplodon densirostris, Ziphius cavirostris*)		
Biomass	0.003906 $t \cdot km^{-2}$	Density and abundance estimates based on boat surveys (INCOGEO 2010, Freitas et al. 2014, Nicolau et al. 2014, Sambolino et al. 2017) Individual body weight (Trites & Pauly 1998)
P/B	0.04 $year^{-1}$	Alves et al. 2014, Morissette et al. 2010
Q/B	9.92 $year^{-1}$	Morissette et al. 2010
EE	Estimated by the model	
Diet		Martins et al. 1985, Hernández-García et al. 1994, Santos et al. 2001, MacLeod et al. 2003, Blanco et al. 2006, Santos et al. 2006, Beatson 2007, Santos et al. 2007, Ozturk et al. 2007, Mintzer et al. 2008, Fernández et al. 2009, West et al. 2009, Bearzi et al. 2011, West et al. 2017
3. Sperm whale (*Physeter macrocephalus*)		
Biomass	0.055496 $t \cdot km^{-2}$	Density and abundance estimates based on boat surveys (INCOGEO 2010, Nicolau et al 2014, Fais et al. 2016) Individual body weight (Trites & Pauly 1998)
P/B	0.05 $year^{-1}$	Morissette et al. 2010
Q/B	5.03 $year^{-1}$	Morissette et al. 2010
EE	Estimated by the model	
Diet		Clarke & MacLeod 1974, Clarke et al. 1993, Fernández et al. 2009
4. Killer whales (*Orcinus orca, Pseudorca crassidens*)		
Biomass	0.000253 $t \cdot km^{-2}$	Abundance estimate based on occasional observations reported by boat surveys and other studies (Freitas et al. 2004b, Alves et al. 2006, Freitas et al. 2012, Nicolau et al. 2014, Alves et al. 2018) Individual body weight (Trites & Pauly 1998)
P/B	0.02 $year^{-1}$	Morissette et al. 2010
Q/B	7.76 $year^{-1}$	Morissette et al. 2010
EE	Estimated by the model	

Diet		Sekiguchi et al. 1992, Alonso et al. 1999, Hernández-García et al. 2002
5. Dolphins (*Delphinus delphis, Stenella frontalis, Stenella coeruleoalba, Steno bredanensis, Tursiops truncatus*)		
Biomass	0.008612 $t \cdot km^{-2}$	Density and abundance estimates based on boat surveys (INCOGEO 2010, Santos et al. 2012, Freitas et al. 2014, Nicolau et al. 2014, Sambolino et al. 2017) Individual body weight (Trites & Pauly 1998)
P/B	0.05 $year^{-1}$	Morissette et al. 2010
Q/B	13.74 $year^{-1}$	Morissette et al. 2010
EE	Estimated by the model	
Diet		Blanco et al. 2001, Clua & Grosvalet 2001, Ringelstein et al. 2006, Pusineri et al. 2007, Dinis et al. 2008, Perrin et al. 2008, Brophy et al. 2009, Fernández et al. 2009, Perrin 2009, Aznar et al. 2017, Giménez et al. 2017, Giménez et al. 2018
6. Monk seal (*Monachus monachus*)		
Biomass	0.000023 $t \cdot km^{-2}$	Abundance estimate based on local observations (Pires et al. 2008, 2011, Karamanlidis et al. 2016) Individual body weight (Trites & Pauly 1998)
P/B	0.08 $year^{-1}$	Piroddi et al. 2015
Q/B	13.15 $year^{-1}$	Piroddi et al. 2015
EE	Estimated by the model	
Diet		Karamanlidis et al. 2011, Pierce et al. 2011, Tonay et al. 2016
7. Shearwaters (*Ardenna gravis, Calonectris diomedea, Puffinus lherminieri, Puffinus puffinus*)		
Biomass	0.000023 $t \cdot km^{-2}$	Abundance estimates based on census at breeding colonies or at-sea counts (Martín et al. 1987, Geraldes 2000, Lorenzo et al. 2003, Rodríguez et al. 2003, Oliveira & Menezes 2004, Granadeiro et al. 2006, Lorenzo & Barone 2007, Catry et al. 2010, SPNM 2015a, SPNM 2015b, Birdlife International 2018) Spatial and temporal distribution (Mougin & Jouanin 1997, Carlsson & Holmström 2004, Nunes et al. 2010, Rodríguez et al. 2010, Catry et al. 2011, Reyes-González et al. 2011, 2012, Rodríguez & Arcos 2012, Ramos et al. 2013, Meirinho et al. 2014, Campioni et al. 2015, Ramos et al. 2015a, Paiva et al. 2016, Alonso et al. 2018). Individual body weight (Robertson & James 1988, Granadeiro 1993, Shoji et al. 2015, Ronconi et al. 2018)
P/B	0.09 $year^{-1}$	Based on annual survival rates from Harris 1966, Perrins et al. 1973, Ramos et al. 2012
Q/B	42.72 $year^{-1}$	Calculated with consumption equation from Daunt et al. (2008) and prey energy densities from Glaser et al. (2015) and Spitz et al. (2010)
EE	Estimated by the model	
Diet		Brown et al. 1981, Thompson 1987, Monteiro et al. 1996, Paiva et al. 2010, Alonso et al. 2014, Ramos et al. 2015a, Alonso et al. 2018
8. Small petrels (*Bulweria bulwerii, Hydrobates castro, Pelagodroma marina, Pterodroma deserta, Pterodroma madeira*)		
Biomass	0.000023 $t \cdot km^{-2}$	Abundance estimates based on census at breeding colonies or at-sea counts (Hernández et al. 1990, Zino & Biscoito 1994, Campos & Granadeiro 1999, Biscoito & Zino 2002, Barone & Delgado 2002, Rodríguez et al. 2003, Oliveira & Menezes 2004, Ramos & Trujillo 2004, Barone & Trujillo 2007, Luzardo et al. 2008, Catry et al. 2010, Menezes et al. 2010, Lorenzo & Rodríguez 2011, Menezes et al. 2011, Catry et al. 2015, SPNM 2015a) Spatial and temporal distribution (Ramírez et al. 2013, Rodríguez et al. 2013, Dias et al. 2015, 2016)

		Individual body weight (Zino & Zino 1986, Robertson & James 1988, Nunes 2000)
P/B	0.19 $year^{-1}$	Based on annual survival rates from Warham 1996, Oro et al. 2005, Ramos et al. 2015b, Ramos et al. 2016
Q/B	91.24 $year^{-1}$	Calculated with consumption equation from Daunt et al. 2008
EE	Estimated by the model	
Diet		Spear et al. 2007, Waap 2015, Waap et al. 2017

9. Coastal birds (*Larus michahellis, Sterna hirundo*)

Biomass	0.000023 $t \cdot km^{-2}$	Abundance estimates based on census at breeding colonies or at-sea counts (Oliveira & Menezes 2004 Catry et al. 2010, Matias & Catry 2010, SPNM 2015b) Individual body weight (Matias & Catry 2010)
P/B	0.05 $year^{-1}$	Based on annual survival rates from Morais et al. 1998
Q/B	69.73 $year^{-1}$	Calculated with consumption equation from Daunt et al. 2008
EE	Estimated by the model	
Diet		Monteiro et al. 1996, Granadeiro et al. 2002, Catry et al. 2010, Matias & Catry 2010, Pedro et al. 2013, López et al. 2016, Romero et al. 2019

10. Turtles (*Caretta caretta*)

Biomass	0.000516 $t \cdot km^{-2}$	Density estimates based on radiotracking and transects in the closeby Canary archipelago (OAG 2013) Individual body weight (Delgado et al. 2010)
P/B	0.15 $year^{-1}$	Taken from Guénette & Morato 2001
Q/B	3.50 $year^{-1}$	Taken from Guénette & Morato 2001
EE	Estimated by the model	
Diet		Brongersma 1968, Brongersma 1972, Van Nierop & Den Hartog 1984, Frick et al. 2009

11. Pelagic sharks (*Alopias superciliosus, Carcharhinus galapagensis, Isurus oxyrinchus, Lamna nasus, Prionace glauca, Sphyrna zygaena*)

Biomass	Estimated by the model	
P/B	0.27 $year^{-1}$	Taken from Morato et al. 2016
Q/B	1.44 $year^{-1}$	Average value calculated for the group. K and L∞ values for each species taken from Froese & Pauly et al. 2018
EE	0.40	
Diet		Clarke 1996, Preti et al. 2008, 2012, Mendonça 2009, Porsmoguer et al. 2013, 2014, 2015, 2017, Klarian et al. 2018

12. Deep sea sharks (*Centrophorus granulosus, Centrophorus lusitanicus, Centrophorus squamosus, Centrophorus uyato/machiquensis, Centroscymnus coelolepis, Centroscymnus crepidater, Centroscymnus owstonii, Chimaera opalescens, Dalatias licha, Deania calcea, Deania hystricosa, Deania profundorum, Etmopterus princeps, Etmopterus pusillus, Etmopterus spinax, Galeus melastomus, Harriotta haeckeli, Harriotta realeighana, Heptranchias perlo, Hexanchus griseus, Hydrolagus affinis, Mustelus mustelus, Pseudotriakis microdon, Scymnodon ringens, Somniosus rostratus, Squaliolus laticaudus, Zameus squamulosus*)

Biomass	Estimated by the model

P/B	0.51 year^{-1}	Taken from Morato et al. 2016
Q/B	2.01 year^{-1}	Average value calculated for the group. K and L∞ values for each species taken from Froese & Pauly et al. 2018
EE	0.60	
Diet		Mauchline & Gordon 1983a, Cortés et al. 1999, Neiva et al. 2006, Dunn et al. 2010, Pethybridge et al. 2011, Xavier et al. 2012, Navarro et al. 2014, Barría et al. 2015, 2018

13. Rays and skates (*Bathytoshia lata, Dasyatis pastinaca, Gymnura altavela, Mobula birostris, Myliobatis aquila, Pteroplatytrygon violacea, Raja brachyura, Raja maderensis, Rostroraja alba, Taeniura grabata, Torpedo marmorata, Torpedo nobiliana*)

Biomass	Estimated by the model	
P/B	0.22 year^{-1}	Taken from Morato et al. 2016
Q/B	2.29 year^{-1}	Average value calculated for the group. K and L∞ values for each species taken from Froese & Pauly et al. 2018
EE	0.95	
Diet		Morato et al. 2003, Saglam & Bascinar 2008, Follesa et al. 2010, Kadri et al. 2014

14. Bigeye tuna (*Thunnus obesus*)

Biomass	Estimated by the model	
P/B	1.88 year^{-1}	Taken from Couce-Montero et al. 2015
Q/B	6.00 year^{-1}	Value calculated for the species. K and L∞ values taken from Froese & Pauly et al. 2018
EE	0.95	
Diet		Matthews et al. 1977, Kim et al. 1997 Moteki et al. 2001, Bertrand et al. 2002, Young et al. 2010, Vaske-Júnior et al. 2012, Horn et al. 2013, Ménard et al. 2013, Romero (unpublished data)

15. Skipjack tuna (*Katsuwonus pelamis*)

Biomass	Estimated by the model	
P/B	1.43 year^{-1}	Taken from Couce-Montero et al. 2015
Q/B	10.40 year^{-1}	Value calculated for the species. K and L∞ values taken from Froese & Pauly et al. 2018
EE	0.95	
Diet		Thomas 1962, Nakamura 1965, Batts 1972, Ankenbrandt 1985, Roger 1994, Ramos 1995, Ménard et al. 2003, Fofandi et al. 2012, Mendizabal 2013, Alatorre-Ramirez et al. 2017, Romero (unpublished data)

16. Other tunas *(Auxis rochei, Thunnus alalunga, Thunnus albacares, Thunnus thynnus*)

Biomass	Estimated by the model	
P/B	0.96 year^{-1}	Taken from Couce-Montero et al. 2015
Q/B	8.07 year^{-1}	Average value calculated for the group. K and L∞ values for each species taken from Froese & Pauly et al. 2018
EE	0.95	Assumption

Diet		Matthews et al. 1977, Allain 2004, Potier et al. 2004, 2007, Satoh et al. 2004, Pusineri et al. 2005, Mostarda et al. 2007, Consoli et al. 2008, Karakulak et al. 2009, Young et al. 2010, Goñi et al. 2011, Battaglia et al. 2013, Horn et al. 2013, Olson et al. 2014

17. Large pelagic fish (*Acanthocybium solandri, Coryphaena equiselis, Coryphaena hippurus, Kajidia albida, Makaira nigricans, Tetrapterus georgii, Tetrapterus pfluegeri, Xiphias gladius*)

Biomass	Estimated by the model	
P/B	0.73 $year^{-1}$	Taken from Morato et al. 2016
Q/B	5.27 $year^{-1}$	Average value calculated for the group. W∞ taken from Froese & Pauly et al. 2018
EE	0.95	Assumption
Diet		Brock 1984, Guerra et al. 1993, Hernández-García V 1995, Massutí et al. 1998, Moteki et al. 2001, Olson & Magaña 2002, Allain 2003, Satoh et al. 2004, Vaske-Junior et al. 2004, Shimose et al. 2006, Pinheiro et al. 2010, Runderhausen et al. 2010, Veiga et al. 2011, Silva et al. 2014, Tripp-Valdez et al. 2015, Brewton et al. 2016, Rosa-Luís et al. 2017

18. Medium pelagic fish (*Caranx crysos, Caranx rhonchus, Decapterus macarellus, Decapterus punctatus, Pomatomus saltatrix, Pseudocaranx dentex, Sarda sarda, Seriola dumerili, Seriola fasciata, Seriola rivoliana, Sphyraena viridensis, Trachinotus ovatus*)

Biomass	Estimated by the model	
P/B	0.87 $year^{-1}$	Taken from Morato et al. 2016
Q/B	3.93 $year^{-1}$	Average value calculated for the group. W∞ taken from Froese & Pauly et al. 2018
EE	0.95	Assumption
Diet		Barreiros et al. 2002, 2003, Campo et al. 2006

19. Chub mackerel (*Scomber colias*)

Biomass	Estimated by the model	
P/B	1.98 $year^{-1}$	Taken from Couce-Montero et al. 2015
Q/B	5.60 $year^{-1}$	Value calculated for the species. W∞ taken from Froese & Pauly et al. 2018
EE	0.95	Assumption
Diet		Habashi & Wojciechowski 1973, Weiss 1974, Castro 1993, Castro & Santana 1994, Castro 1995, Whabi et al. 2015, Gushchin & Corten 2017, Vieira (unpublished data)

20. Blue jack mackerel (*Trachurus picturatus*)

Biomass	Estimated by the model	
P/B	1.76 $year^{-1}$	Taken from Vasconcelos et al. 2018
Q/B	6.50 $year^{-1}$	Value calculated for the species. W∞ taken from Froese & Pauly et al. 2018
EE	0.95	Assumption
Diet		Olaso et al. 1999, Cabral & Murta 2002, Gushchin & Corten 2017, Hirch & Christhiansen 2010, Vieira (unpublished data)

21. Small pelagic fish (*Atherina presbyter, Boops boops, Macrorhamphosus scolopax* (juveniles), *Sardina pilchardus, Sardinella maderensis, Scomberesox saurus, Trachurus trachurus*)		
Biomass	Estimated by the model	
P/B	1.98 year^{-1}	Taken from Morato et al. 2016
Q/B	16.03 year^{-1}	Average value calculated for the group. K and L∞ values for each species taken from Froese & Pauly et al. 2018
EE	0.95	Assumption
Diet		Moreno & Castro 1995, Fock et al. 2002, Matthiessen et al. 2003, Christiansen et al. 2009, Hirch & Christhiansen 2010, Guschin & Corten 2017
22. Epipelagic fish (*Balistes* sp. (juveniles), *Cheilopogon exsiliens, Cheilopogon pinnatibarbatus, Coryphaena* sp. (juveniles), *Exocoetus volitans, Naucrates ductor, Seriola* sp. (juveniles), *Lagocephalus lagocephalus, Ranzania laevis, Sphoeroides pachygaster*)		
Biomass	Estimated by the model	
P/B	0.83 year^{-1}	Taken from Morato et al. 2016
Q/B	5.35 year^{-1}	Average value calculated for the group. K and L∞ values for each species taken from Froese & Pauly et al. 2018
EE	0.95	Assumption
Diet		Deudero 2001, Deudero & Morales-Nin 2001, Cassaza 2008, Febyanti & Syahailatua 2008
23. Large reef-associated fish (*Enchelycore anatina, Epinephelus marginatus, Gymnothorax unicolor, Muraena augusti, Mycteroperca fusca*)		
Biomass	Estimated by the model	
P/B	0.44 year^{-1}	Taken from Morato et al. 2016
Q/B	3.42 year^{-1}	Average value calculated for the group. K and L∞ values for each species taken from Froese & Pauly et al. 2018
EE	0.95	Assumption
Diet		Azevedo et al. 1995, Barreiros & Santos 1998, Reñones et al. 2002, Soares et al. 2003, Sallami et al. 2014, Zaidi et al. 2017
24. Medium reef-associated fish (*Balistes capriscus, Bodianus scrofa, Canthidermis sufflamen, Chelon labrosus, Chelon ramada, Diplodus cervinus, Diplodus sargus, Diplodus vulgaris, Kyphosus sectatrix, Labrus bergylta, Oblada melanura, Sarpa salpa, Sparisoma cretense*)		
Biomass	Estimated by the model	
P/B	1.26 year^{-1}	Taken from Morato et al. 2016
Q/B	12.14 year^{-1}	Average value calculated for the group. K and L∞ values for each species taken from Froese & Pauly et al. 2018
EE	0.95	Assumption
Diet		Whitehead et al. 1984, Azevedo 1995, Porteiro et al. 1996, Figueiredo et al. 2005, Espino et al. 2015, Friedlander et al. 2016, 2017
25. Small reef-associated fish (*Abudefduf luridus, Apogon imberbes, Aulostomus strigosus, Canthigaster capistrata, Chromis limbata, Coris julis, Coryphoblennius galerita, Gobius paganellus, Heteropriacanthus cruentatus, Lepadogaster candolii, Lepadogaster lepadogaster, Mauligobius maderensis*,		

	Ophioblennius atlanticus, Parablennius parvicornis, Sphoeroides marmoratus, Stephanolepis hispidus, Symphodus trutta, Thalassoma pavo, Tripterygion delaisi)	
Biomass	Estimated by the model	
P/B	2.49 year^{-1}	Taken from Morato et al. 2016
Q/B	17.53 year^{-1}	Average value calculated for the group. K and L∞ values for each species taken from Froese & Pauly et al. 2018
EE	0.95	Assumption
Diet		Azevedo 1995, Porteiro et al. 1996, Mancera-Rodríguez & Castro-Hernández 2015, Friedlander et al. 2016, 2017
26. Medium benthopelagic fish (*Dentex dentex, Dentex gibbosus, Pagellus acarne, Pagellus bogaraveo, Pagellus erythrinus, Pagrus pagrus, Spondyliosoma cantharus*)		
Biomass	Estimated by the model	
P/B	1.01 year^{-1}	Taken from Pajuelo & Lorenzo 1998, Pajuelo & Lorenzo 2000
Q/B	4.29 year^{-1}	Average value calculated for the group. K and L∞ values for each species taken from Froese & Pauly et al. 2018
EE	0.95	Assumption
Diet		Gonçalves & Erzini 1998, Labropoulou et al. 1999, Morato et al. 2001, El-Fergani & El-Mor 2014
27. Benthic fish (*Arnoglossus imperialis, Arnoglossus rueppelii, Apterichtus caecus, Aulopus filamentosus, Bothus podas, Chelidonichthys cuculus, Chelidonichthys lastoviza, Chelidonichthys lucerna, Chelidonichthys obscures, Echiichthys vipera, Lepidorhombus boscii, Lepidotrigla dieuzeidei, Microchirus azevia, Microchirus ocellatus, Mullus surmuletus, Pegusa lascaris, Synchiropus phaeton, Synodus saurus, Synodus synodus, Symphurus insularis, Trachinus draco, Uranoscopus scaber*)		
Biomass	Estimated by the model	
P/B	1.08 year^{-1}	Taken from Malta et al. 2018
Q/B	5.87 year^{-1}	Average value calculated for the group. K and L∞ values for each species taken from Froese & Pauly et al. 2018
EE	0.95	Assumption
Diet		Azevedo 1995, Labropoulou et al. 1997, Teixeira et al. 2009, 2010, Hirch et al. 2010
28. Large demersal fish (*Conger conger, Gymnothorax bacalladoi, Gymnothorax maderensis, Gymnothorax polygonius, Phycis blennoides, Phycis phycis, Polyprion americanus*)		
Biomass	Estimated by the model	
P/B	0.57 year^{-1}	Taken from Morato et al. 2016
Q/B	2.88 year^{-1}	Average value calculated for the group. K and L∞ values for each species from Froese & Pauly et al. 2018
EE	0.95	Assumption
Diet		Morato et al. 1999, Young & Winn 2003
29. Medium demersal fish (*Beryx decadactylus, Beryx splendens, Gephyroberyx darwini, Helicolenus dactylopterus, Pontinus kuhlii, Scorpaena scrofa, Setarches guentherii*)		
Biomass	Estimated by the model	
P/B	0.34 year^{-1}	Taken from Couce-Montero et al. 2015, Morato et al. 2016

Q/B	3.67 year^{-1}	Average value calculated for the group. K and L∞ values for each species taken from Froese & Pauly et al. 2018
EE	0.95	Assumption
Diet		Morato et al. 1998, Dürr & González 2002, Cabiddu et al. 2010

30. Small demersal fish (*Gaidropsarus granti*, *Scorpaena canariensis*, *Scorpaena maderensis*, *Scorpaena notata*, *Serranus atricauda*, *Serranus cabrilla*)

Biomass	Estimated by the model	
P/B	1.23 year^{-1}	Taken from Couce-Montero et al. 2015
Q/B	6.30 year^{-1}	Average value calculated for the group. K and L∞ values for each species taken from Froese & Pauly et al. 2018
EE	0.95	Assumption
Diet		Morato et al. 2001, Morte et al. 2001

31. Black-scabbard fish (*Aphanopus carbo*, *Aphanopus intermedius*)

Biomass	Estimated by the model	
P/B	0.53 year^{-1}	Taken from Guénette & Morato 2001
Q/B	2.52 year^{-1}	Average value calculated for the group. W∞ taken from Froese & Pauly et al. 2018
EE	0.95	Assumption
Diet		Maul 1961, Clarke & Lu 1995, Freitas 1998, Farias et al. 2014

32. Large benthopelagic fish (*Alepisaurus ferox, Benthodesmus simonyi, Lepidocybium flavobrunneum, Lepidopus caudatus, Promethichthys prometheus, Ruvettus pretiosus, Serrivomer beanii, Serrivomer lanceolatoides*)

Biomass	Estimated by the model	
P/B	0.57 year^{-1}	Average value calculated for the group based on species-specific values from Guénette & Morato 2001, Couce-Montero 2015, Morato et al. 2016
Q/B	2.04 year^{-1}	Average value calculated for the group. W∞ taken from Froese & Pauly et al. 2018
EE	0.95	Assumption
Diet		Matthews 1977, Clarke & Lu 1995, Lorenzo & Pajuelo 1995, Morato et al. 1998, Moteki 2001, Klimpel et al. 2006, Vasilakopoulos et al. 2011, Viana et al. 2012, Choy et al. 2013

33. Medium benthopelagic fish (*Arctozenus risso, Brama brama, Diplospinus multistriatus, Gadella imberbes, Gadella maraldi, Hoplostethus atlanticus, Laemonema robustum, Lepidion guentheri, Lestidiops jayakari, Macroparalepis nigra, Magnisudis atlantica, Mora moro, Physiculus dalwigki, Schedophilus medusophagus, Schedophilus ovalis, Scopelosaurus argenteus, Sudis hialina, Taractichthys longipinnis, Zenopsis conchifera*)

Biomass	Estimated by the model	
P/B	0.30 year^{-1}	Taken from Guénette & Morato 2001
Q/B	3.28 year^{-1}	Average value calculated for the group. W∞ taken from Froese & Pauly et al. 2018
EE	0.95	Assumption
Diet		Mauchline & Gordon 1980, Rosecchi et al. 1988, Bulman & Koslow 1992, Pierrot-Bults 1998, Garibaldi et al. 2010, Yang 2011, Battaglia et al. 2014, Anastasopoulou et al. 2018

34. Small benthopelagic fish (*Anthias antias, Antigonia capros, Callanthias ruber, Capros aper, Centracanthus cirrus, Chlorophthalmus agassizi, Diretmoides pauciradiatus, Hoplostethus mediterraneus, Macrorhamphosus scolopax*)

Biomass	Estimated by the model	
P/B	1.20 year^{-1}	Taken from Guénette & Morato 2001
Q/B	5.52 year^{-1}	Average value calculated for the group. W∞ taken from Froese & Pauly et al. 2018
EE	0.95	Assumption
Diet		Fock et al. 2002, Pais 2002, Matthiessen et al. 2003, Christiansen et al. 2009, Hirch & Christhiansen 2010

35. Myctophids (*Benthosema suborbital, Bolinichthys indicus, Ceratoscopelus maderensis, Ceratoscopelus warmingii, Diaphus adenomus, Diaphus dumerilii, Diaphus holti, Diaphus metopoclampus, Diaphus mollis, Diaphus perspicillatus, Diaphus rafinesquii, Diaphus termophilus, Diogenichthys atlanticus, Electrona risso, Gonichthys cocco, Hygophum benoiti, Hygophum hygomii, Hygophum reinhardtii, Hygophum taaningi, Lampadena chavesi, Lampanyctus alatus, Lampanyctus ater, Lampanyctus festivus, Lampanyctus intricarius, Lampanyctus photonotus, Lampanyctus pusillus, Lepidophanes gaussi, Lobianchia dofleini, Lobianchia gemellarii, Myctophum nitidulum, Myctophum punctatum, Myctophum selenops, Nannobrachium atrum, Notolychnus valdiviae, Notoscopelus bolini, Notoscopelus resplendens, Symbolophorus veranyi, Taaningichthys bathyphilus, Taaningichthys minimus*)

Biomass	Estimated by the model	
P/B	1.76 year^{-1}	Average value calculated for the group. K and L∞ values for each species from Froese & Pauly et al. 2018
Q/B	13.88 year^{-1}	Average value calculated for the group. W∞ taken from Froese & Pauly et al. 2018
EE	0.95	Assumption
Diet		Clarke 1980, Podrazhanskaya 1993, Bernal et al. 2013

36. Small mesopelagic fish (*Argyropelecus aculeatus, Argyropelecus hemigymnus, Argyropelecus gigas, Bonapartia pedaliota, Cyclothone braueri, Cyclothone microdon, Cyclothone pallida, Cyclothone pseudopallida, Diplophos taenia, Diretmichthys parini, Diretmus argenteus, Gonostoma atlanticum, Gonostoma denudatum, Ichthyococcus ovatus, Margrethia obtusirostra, Maurolicus muelleri, Neoscopelus macrolepidotus, Neoscopelus microchir, Notoscopelus bolini, Sigmops elongate, Sternoptyx diaphana, Sternoptyx pseudobscura, Valenciennellus tripunctulatus, Vinciguerria attenuata, Vinciguerria nimbaria, Vinciguerria poweriae)*

Biomass	Estimated by the model	
P/B	2.27 year^{-1}	Average value calculated for the group. K and L∞ values for each species from Froese & Pauly et al. 2018
Q/B	14.34 year^{-1}	Average value calculated for the group. W∞ taken from Froese & Pauly et al. 2018
EE	0.95	Assumption
Diet		Merrett & Roe 1974, Mauchline & Gordon 1983b, Gordon et al. 1985, Hopkins & Baird 1985, Uchikawa et al. 2001a, , Uchikawa et al. 2001b, Carmo et al. 2015

37. Large bathydemersal fish (*Histiobranchus bathybius, Saccopharynx ampullaceus, Simenchelys parasitica, Synaphobranchus affinis, Synaphobranchus kaupii*)

Biomass	Estimated by the model	
P/B	0.42 year^{-1}	Average value calculated for the group. K and L∞ values for each species from Froese & Pauly et al. 2018
Q/B	2.98 year^{-1}	Average value calculated for the group. W∞ taken from Froese & Pauly et al. 2018
EE	0.95	Assumption

Diet		Merrett & Domansky 1985, Houston & Haedrich 1986, Gordon & Duncan 1987, Saldanha et al. 1995, Gordon & Mauchline 1996, Martin & Christhiansen 1997, Marques 1998

38. Medium bathydemersal fish1 (*Coryphaenoides rupestris, Epigonus telescopus, Lyconus brachycolus, Malacocephalus laevis, Polymixia nobilis, Trachyrincus scabrus*)

Biomass	Estimated by the model	
P/B	0.30 $year^{-1}$	Taken from Guenette & Morato 2001, Morato et al. 2016
Q/B	2.23 $year^{-1}$	Average value calculated for the group. W∞ taken from Froese & Pauly et al. 2018
EE	0.95	Assumption
Diet		Mauchline & Gordon 1984a, Macpherson & Ruel 1987, Houston & Haedrich 1986, García-Mederos et al. 2010

39. Medium bathydemersal fish2 (*Aldrovandia affinis, Alepocephalus bairdii, Alepocephalus rostratus, Antimora rostrata, Bajacalifornia megalops, Bathygadus favosus, Bathygadus melanobranchus, Cataetyx laticeps, Coelorinchus labiatus, Conocara salmoneum, Coryphaenoides armatus, Coryphaenoides leptolepis, Coryphaenoides mediterraneus, Coryphaenoides profundicolus Coryphaenoides rudis, Echinomacrurus mollis, Gadomus arcuatus, Halosauropsis macrochir, Halosaurus johnsonianus, Halosaurus ovenii, Hymenocephalus italicus, Hymenogadus gracilis, Lyconus brachycolus, Nezumia aequalis, Nezumia longebarbata, Nezumia sclerorhynchus, Spectrunculus grandis*)

Biomass	Estimated by the model	
P/B	0.35 $year^{-1}$	Taken from Morato et al. 2016
Q/B	2.42 $year^{-1}$	Average value calculated for the group. W∞ taken from Froese & Pauly et al. 2018
EE	0.95	Assumption
Diet		Sedberry & Musick 1978, Mauchline & Gordon 1983b, Mauchline & Gordon 1984a, Gordon & Duncan 1987, Houston & Haedrich 1986, Carrassón & Matallanas 1998, 2002a, 2002b, Drazen et al. 2008, Sever et al. 2008, Fanelli & Cartes 2010

40. Medium bathypelagic fish (*Astronesthes gemmifer, Astronesthes micropogon, Avocettina infans, Bathophilus digitatus, Bathophilus vaillanti, Benthalbella infans, Borostomias antarcticus, Chauliodus danae, Chauliodus sloani, Chiasmodon niger, Chirostomias pliopterus, Echiostoma barbatum, Eurypharynx pelecanoides, Eustomias obscurus, Evermannella melanoderma, Idiacanthus fascíola, Leptostomias gladiator, Malacosteus niger, Melanonus zugmayeri, Melanostomias tentaculatus, Photonectes braueri, Photostomias guernei, Rhadinesthes decimus, Stomias boa, Stomias longibarbatus*)

Biomass	Estimated by the model	
P/B	0.56 $year^{-1}$	Average value calculated for the group. K and L∞ values for each species from Froese & Pauly et al. 2018
Q/B	4.46 $year^{-1}$	Average value calculated for the group. W∞ taken from Froese & Pauly et al. 2018
EE	0.95	Assumption
Diet		Mauchline & Gordon 1983b, Sutton & Hopkins 1996, Butler et al. 2001, Gaskett et al. 2001, Sutton 2005, Prokofiev & Kukuev 2009, Yang et al. 2011, Battaglia et al. 2018

41. Small bathypelagic/demersal fish (*Barbantus curvifrons, Bathylagichthys greyae, Bathymicrops regis, Bathypterois longipes, Cetomimus hempeli, Cetostoma regaini, Chaunax pictus, Chaunax suttkusi, Chlorophthalmus agassizi, Dolicholagus longirostris, Epigonus constanciae, Holtbyrnia macrops, Howella atlantica, Laemonema yarrellii, Maulisia mauli , Melamphaes typhlops, Melanolagus bericoides, Opisthoproctus soleatus, Platyberyx opalescens, Poromitra capito, Rouleina maderensis, Rinoctes nasutus, Searsia koefoedi, Scopelogadus beanie, Xenodermichthys copei*)

Biomass	Estimated by the model	
P/B	0.70 $year^{-1}$	Average value calculated for the group. K and L∞ values for each species from Froese & Pauly et al. 2018

Q/B	5.91 year^{-1}	Average value calculated for the group. W∞ taken from Froese & Pauly et al. 2018
EE	0.95	Assumption
Diet		Mauchline & Gordon 1983b, Mauchline & Gordon 1984c, Roe & Badcock 1984, Gartner & Musick 1989, Novotny 2018, Woodstock 2018

42. Small epipelagic cephalopods *(Ommastrephes bartramii, Sthenoteuthis pteropus, Todarodes sagittatus, Onychoteuthis banksii, Cranchia scabra, Argonauta argo, Japetella diaphana, Tremoctopus violaceus)*

Biomass	Estimated by the model	
P/B	8.50 year^{-1}	Taken from Pinkerton 2011
Q/B	25.00 year^{-1}	Taken from Pinkerton 2011
EE	0.95	Assumption
Diet		Piatkwovsky et al. 1998, Watanabe et al. 2008, Parry 2006

43. Small mesopelagic cephalopods (*Abraliopsis pfefferi, Abraliopsis morisii, Abraliopsis gilchristi, Enoploteuthis anapsis, Histioteuthis arcturi, Histioteuthis meleagroteuthis, Histioteuthis corona, Pyroteuthis margaritifera, Pterygioteuthis giardi, Pterygioteuthis gemmata, Liocranchia reinhardti, Helicocranchia pfefferi, Taonius pavo, Megalocranchia oceánica, Bathothauma lyromma, Leachia atlantica, Idioteuthis hjorti, Mastigoteuthis magna, Mastigoteuthis schmidti, Heteroteuthis dispar, Brachioteuthis picta, Brachioteuthis riisei, Chtenopteryx sicula, Chtenopteryx canariensis, Onykia robsoni, Thysanoteuthis rhombus, Chiroteuthis veranyii)*

Biomass	Estimated by the model	
P/B	4.45 year^{-1}	Taken from Morato & Pitcher et al. 2002
Q/B	16.86 year^{-1}	Taken from Morato & Pitcher et al. 2002
EE	0.95	Assumption
Diet		Passarella & Hopkins 1991

44. Large mesopelagic cephalopods (*Architeuthis sp., Todarodes sagittatus, Lepidoteuthis grimaldii, Taningia danae, Haliphron atlanticus, Moroteuthis robsoni, Cycloteuthis sirventi and Ancistrocheirus lesueurii)*

Biomass	Estimated by the model	
P/B	2.50 year^{-1}	Taken from Morato & Pitcher et al. 2002
Q/B	10.00 year^{-1}	Taken from Morato & Pitcher et al. 2002
EE	0.95	Assumption
Diet		Bolstad & O'Shea 2004, Watanabe et al. 2008, Parry 2006

45. Crabs (*Plagusia depressa, Percnon gibbesi, Grapsus grapsus, Calcinus tubularis, Dardanus calidus, Pagurus cuanensis, Palinurus elephas, Galathea squamifera, Scyllarides latus, Scyllarides latus, Maja squinado and Pagurus anachoretus, Chaceon affinis, Paromola cuvieri, Spinolambrus macrochelos)*

Biomass	Estimated by the model	
P/B	1.60 year^{-1}	Taken from Morato & Pitcher et al. 2002
Q/B	10.00 year^{-1}	Taken from Morato & Pitcher et al. 2002

EE	0.95	Assumption
Diet		Morato et al. 2016

46. Shrimps (*Plesionika edwardsii, P. ensis, P. narval, Heterocarpus ensifer, H. laevigatus, H. grimaldii, Acanthephyra eximia, Benthesicymus bartletti, Lepas anatifera, Lepas anserifera, Lepas pectinata, Alepas pacifica and Dosima fascicularis, Planes minutes)*

Biomass	Estimated by the model	
P/B	1.45 $year^{-1}$	Average value calculated for the group based on species-specific values from Couce-Montero et al. (2015), Morato et al. (2016) and Torres et al. (2013)
Q/B	11.74 $year^{-1}$	Average value calculated for the group based on species-specific values from Couce-Montero et al. (2015), Morato et al. (2016) and Torres et al. (2013)
EE	0.95	Assumption
Diet		Cartes et al. 1993, Labropoulou & Kostikas 1999

47. Echinoderms (*Asteroidea, Ophiuroidea, Crinoidea, Echinoidea and Holothuroidea: inc. Antedon bifida, Arbacia lixula, Astropecten irregulares, Centrostephanus longispinus, Coscinasterias tenuispina, Diadema africana, Echinaster sepositus, Endoxocrinus wyvillethomsoni, Holothuria sanctori, Luidia ciliaris,Ophioderma longicauda, Paracentrotus lividus, Sphaerechinus granularis, Stylocidaris affinis)*

Biomass	Estimated by the model	
P/B	1.72 $year^{-1}$	Couce-Montero et al. 2015
Q/B	6.91 $year^{-1}$	Couce-Montero et al. 2015
EE	0.85	Assumption
Diet		Christensen 1970, Brun 1972, Franz & Worley 1982, Beddingfield & McClintock 1993, de Juan et al. 2007

48. Suprabenthic zooplânkton (inc. *copepods, amphipods, isopods, euphasiids and mysids*)

Biomass	Estimated by the model	
P/B	16.00 $year^{-1}$	Average value from Sanchéz & Olaso 2004, Torres et al. 2013
Q/B	42.00 $year^{-1}$	Average value from Sanchéz & Olaso 2004, Torres et al. 2013
EE	0.95	Assumption
Diet		Based on Sanchéz & Olaso 2004, Torres et al. 2013

49. Mollusks (*Trochidae, Littorinidae, Patellidae, Siphonoridae, Haliotidae, Columbellidae, Aplysiidae, Cerithidae*)

Biomass	Estimated by the model	
P/B	0.90 $year^{-1}$	Couce-Montero et al. 2015
Q/B	5.50 $year^{-1}$	Couce-Montero et al. 2015
EE	0.85	Assumption
Diet		Based on Couce-Montero et al. 2015

50. Other benthos (*polychaets, annelids and other benthic invertebrates*)

Biomass	Estimated by the model

P/B	2.74 $year^{-1}$	Average value from Olaso & Sanchéz 2004, Torres et al. 2013, Morato et al. 2016
Q/B	12.25 $year^{-1}$	Average value from Olaso & Sanchéz 2004, Torres et al. 2013, Morato et al. 2016
EE	0.95	Assumption
Diet		Based on Guénette & Morato 2001

51. Jellyfish (*jellyfishes and hydrozoans (e.g., Pelagia noctiluca, Physalia physalis)*)

Biomass	Estimated by the model	
P/B	13.87 $year^{-1}$	Malej 1989, Coll et al. 2006, Torres et al. 2013
Q/B	50.48 $year^{-1}$	Malej 1989, Coll et al. 2006, Torres et al. 2013
EE	0.95	Assumption
Diet		Rosa et al. 2013, Tilves et al. 2016

52. Sessile filter feeders (*sponges, hard corals, soft corals (gorgonian corals), cold-water corals (inc. anthipatharian corals), anemons, ascidians and polypoid hydrozoans*)

Biomass	Estimated by the model	
P/B	0.80 $year^{-1}$	Optiz et al. 1993, Morato & Pitcher 2002
Q/B	9.00 $year^{-1}$	Optiz et al. 1993, Morato & Pitcher 2002
EE	0.50	Assumption
Diet		Based on Morato & Pitcher 2002

53. Large-sized zooplânkton (*This group consists of zooplankton > 5mm, namely crustaceans such as decapod's larvae and some euphasiids, but also chaetognaths, ctenophors, pteropods, fish larvae and free-swimming tunicates, such as appendicularians or salps*)

Biomass	Estimated by the model	
P/B	8.70 $year^{-1}$	Morato et al. 2009
Q/B	29.00 $year^{-1}$	Morato et al. 2009
EE	0.95	Assumption
Diet		Based on Morato et al. 2009

54. Small-sized zooplânkton (*This group consists of zooplankton < 5mm, namely crustaceans such as copepods, ostracods, amphipods and mysids, but also Radiolaria, bivalve larvae and small tunicates, chaetognaths and ctenophors*)

Biomass	10.900000 $t \cdot km^{-2}$	
P/B	11.21 $year^{-1}$	Morato et al. 2009
Q/B	43.29 $year^{-1}$	Morato et al. 2009
EE	Estimated by the model	Assumption
Diet		Based on Guénette & Morato 2001

55. Macroalgae (inc. *Asparagopsis armata, Asparagopsis taxiformis, Caulerpa webbiana,Chaetomorpha sp., Codium adhaerens, Corallina elongata, Cottoniella filamentosa, Cryptopleura ramosa, Cystoseira marina, Dasycladus vermicularis, Dictyota fasciola, Dictyota neglecta, Halopteris scoparia, Jania rubens,*

	Laminaria ochroleuca, Laurencia viridis, Lobophora variegata, Lophocladia trichoclados, Padina pavonica, Pterocladia capillacea, Pseudotetraspora marina, Sargassum filipendula, Stypopodium zonale, Symploca hydnoides, Ulva lactula, Ulva rigida, Valonia utricularis, Zonaria tournefourtii)	
Biomass	Estimated by the model	
P/B	27.95 $year^{-1}$	Couce-Montero et al. 2015
Q/B	-	
EE	0.50	Assumption
Diet	-	
56. Phytoplânkton (inc. diatoms, dinoflagellates and coccolithophores)		
Biomass	9.320000 $t \cdot km^{-2}$	
P/B	121.82 $year^{-1}$	Calculated dividing the annual primary production by the annual mean biomass
Q/B	-	
EE	Estimated by the model	Assumption
Diet	-	
Other parameters		Integrated Chl-a concentration (0-150m of depth) of 0.932 g C m^{-2} (Mendonça et al. 2012) Primary production of 113.5391 g C $m^{-2} \cdot year^{-1}$ (Kleisner & Hoornaert 2015)
57. Detritus		
Biomass	21.809400 $t \cdot km^{-2}$	Calculated with empirical equation from Pauly et al. 1993
P/B	-	
Q/B	-	
EE	Estimated by the model	
Diet	-	
Other parameters		Average euphotic zone of 118m (Christhiansen et al. 2010) Primary production of 113.5391 g C $m^{-2} \cdot year^{-1}$ (Kleisner & Hoornaert 2015)

Table S2 – Diet composition of each functional group of the food web of the oceanic region of the archipelago of Madeira.

Prey \ Predator		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
1	Baleen whales																								
2	Toothed whales				0.05																				
3	Sperm whale																								
4	Killer whales																								
5	Dolphins				0.05							0.10													
6	Monk seal																								
7	Shearwaters																								
8	Small petrels									0.01															
9	Coastal birds																								
10	Turtles				0.05		0.03					0.03													
11	Pelagic sharks																								
12	Deep-sea sharks												0.10												
13	Rays											0.08													
14	Bigeye tuna				0.10																				
15	Skipjack tuna				0.10													0.05							
16	Other tunas																								
17	Pelagic fish L																								
18	Pelagic fish M																	0.05							
19	Chub mackerel	0.10			0.05	0.15		0.25		0.05		0.05			0.20	0.25	0.15	0.15	0.25						
20	Blue Jack mackerel	0.10			0.05	0.15		0.10		0.05		0.10			0.20	0.15	0.15	0.10	0.25						
21	Pelagic fish S	0.20			0.05	0.10		0.20		0.19		0.05		0.05	0.10	0.15	0.10	0.10	0.10	0.35	0.25		0.25		
22	Epipelagic fish S/M				0.10	0.05		0.05								0.10	0.05	0.15	0.15						
23	Reef fish L						0.05																		
24	Reef fish M						0.10							0.05											
25	Reef fish S						0.05			0.05	0.05			0.05					0.15						
26	Benthopelagic fish M1					0.05	0.10						0.05	0.05					0.05						0.05
27	Benthic fish S/M					0.03	0.10							0.15					0.05						0.20
28	Demersal fish L					0.03	0.10																		
29	Demersal fish M						0.05																		
30	Demersal fish S					0.05	0.05							0.05											

Table S2 – Diet composition of each functional group of the food web of the oceanic region of the archipelago of Madeira (continued horizontatlly from page 178)

	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54
1																														
2																														
3																														
4																														
5																														
6																														
7																														
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14																														
15																														
16																														
17																														
18																														
19																														
20				0.05				0.05																						
21		0.25																												
22								0.10																						
23																														
24					0.05																									
25		0.05	0.10	0.15		0.15																								
27				0.05																										
28				0.05	0.05	0.05																								
29																														
30				0.10																										

Table S2 – Diet composition of each functional group of the food web of the oceanic region of the archipelago of Madeira (continued vertically from 178)

Prey \ Predator		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
31	Black scabbard fish												0.05												
32	Benthopelagic fish L2																								
33	Benthopelagic fish M2											0.05	0.05		0.10			0.10							
34	Benthopelagic fish S2					0.05							0.15	0.20	0.05	0.05	0.05								
35	Myctophids	0.10	0.10			0.15		0.05	0.25	0.10	0.05	0.05	0.10		0.10	0.05	0.05	0.10		0.05	0.05				
36	Mesopelagic fish S	0.05	0.15			0.10		0.05	0.20							0.05	0.05								
37	Bathydemersal fish L																								
38	Bathydemersal fish M1												0.05												
39	Bathydemersal fish M2											0.05	0.05												
40	Bathypelagic fish M		0.05										0.10				0.05								
41	Bathydemersal fish S								0.05																
42	Epipelagic cephalopods S	0.05			0.05	0.05		0.20	0.05			0.05				0.05	0.15	0.20		0.05	0.05				
43	Mesopelagic cephalopods S/M		0.60	0.35	0.35	0.05	0.05	0.10	0.15		0.05	0.15	0.25		0.15		0.05								
44	Mesopelagic cephalopods L		0.10	0.65								0.10	0.05												
45	Crabs						0.18			0.25		0.05		0.20										0.10	0.15
46	Shrimps									0.10	0.10	0.10		0.05	0.05	0.05	0.05								
47	Echinoderms																							0.15	
48	Suprabenthic zooplankton																								
49	Mollusks						0.15			0.10															
50	Other benthos																							0.10	0.05
51	Jellyfish										0.65														
52	Sessile filter feeders																								
53	Zooplankton L	0.10							0.20	0.10	0.10			0.10	0.05	0.05	0.10			0.05	0.15	0.05	0.15		
54	Zooplankton S	0.30							0.10					0.05		0.05				0.38	0.45	0.80	0.50		0.20
55	Macroalgae																			0.03		0.05	0.05		0.40
56	Phytoplankton																			0.05		0.05			
57	Detritus																			0.05	0.05	0.05	0.05		0.05

Table S2 – Diet composition of each functional group of the food web of the oceanic region of the archipelago of Madeira (continued vertically from page 179)

	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54
31				0.05				0.05																						
32							0.10	0.10					0.05							0.05										
33				0.20	0.10	0.05	0.20	0.15						0.10				0.10		0.05										
34		0.10			0.15		0.10	0.20	0.15				0.10	0.05		0.45		0.30	0.15	0.25										
35					0.05		0.05	0.15	0.20				0.10			0.20		0.15	0.10	0.15										
36							0.10																							
37				0.05									0.05							0.05										
38							0.10						0.05	0.05		0.05				0.10										
39							0.05	0.05	0.15				0.10			0.10				0.05										
40							0.05						0.05	0.05	0.05	0.10		0.05		0.10										
41								0.05										0.10		0.05										
42		0.05			0.05		0.15	0.05					0.20				0.05	0.10	0.10	0.15										
43							0.10																							
44	0.05		0.20	0.15	0.05	0.40								0.10	0.05															
45			0.05		0.30	0.10			0.05		0.05	0.05	0.15	0.10	0.10	0.10	0.05	0.10	0.05											
46	0.05	0.05	0.05												0.05							0.05								
47		0.05	0.15							0.05	0.05		0.05	0.30	0.25		0.40		0.05		0.10	0.10	0.10	0.05	0.20	0.25				
48		0.05	0.15	0.05	0.05									0.15	0.15						0.15	0.05	0.15		0.05	0.10				
49	0.25	0.10	0.30	0.05		0.05				0.10		0.10		0.05	0.20		0.15				0.10	0.10	0.20			0.10				
50									0.25						0.05															
51																	0.05				0.05		0.05							
52		0.10				0.10		0.05	0.05	0.15	0.05	0.10	0.05		0.05		0.10	0.05	0.10			0.15			0.05	0.05	0.30		0.10		
53	0.30	0.15			0.05	0.05			0.15	0.70	0.75	0.70	0.05	0.05	0.05		0.10	0.05	0.45		0.05	0.25			0.05		0.70	0.20	0.15	
54	0.25																				0.05		0.30		0.10	0.05			0.10	0.15
55											0.05	0.05													0.10			0.10	0.10	0.70
56	0.10	0.05									0.05						0.10				0.50	0.30	0.20	0.95	0.45	0.45		0.70	0.55	0.15

Table S3 - Fisheries data for the Madeira System (2000-2017). S – Small, M – Medium, L – Large

Group name	Purse seine	Scabbard fishery	Tuna pole and line	Bottom longline and handline	Squids fishery	Recreational	Pelagic longline (mainland)	Total	References
Pelagic sharks	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000	0.000025	0.000025	Martins & Ferreira 1995, Severino 2004, Pajuelo et al. 2010
Deep-sea sharks	0.000000	0.000225	0.000000	0.000000	0.000000	0.000000	0.000000	0.000225	https://estatistica.madeira.gov.pt/
Bigeye tuna	0.000000	0.000000	0.002697	0.000000	0.000000	0.000013	0.000000	0.002710	Gouveia et al. 2017
Skipjack tuna	0.000000	0.000021	0.003489	0.000000	0.000000	0.000011	0.000000	0.003520	Gouveia et al. 2017
Other tunas	0.000000	0.000000	0.000279	0.000000	0.000000	0.000004	0.000000	0.000284	Gouveia et al. 2017
Pelagic L	0.000000	0.000011	0.000000	0.000000	0.000000	0.000083	0.000020	0.000115	https://www.ine.pt
Pelagic M	0.000000	0.000000	0.000000	0.000000	0.000000	0.000041	0.000000	0.000041	https://www.ine.pt
Chub mackerel	0.000946	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000	0.000946	https://estatistica.madeira.gov.pt/
Blue Jack mackerel	0.001437	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000	0.001437	https://estatistica.madeira.gov.pt/
Pelagic S	0.000051	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000	0.000051	https://estatistica.madeira.gov.pt/
Reef-associated M	0.000000	0.000000	0.000000	0.000004	0.000000	0.000000	0.000000	0.000004	https://estatistica.madeira.gov.pt/
Benthopelagic M1	0.000000	0.000000	0.000000	0.000060	0.000000	0.000000	0.000000	0.000060	https://estatistica.madeira.gov.pt/
Demersal L	0.000000	0.000000	0.000000	0.000078	0.000000	0.000000	0.000000	0.000078	https://estatistica.madeira.gov.pt/
Demersal M	0.000000	0.000000	0.000000	0.000004	0.000000	0.000000	0.000000	0.000004	https://estatistica.madeira.gov.pt/
Demersal S	0.000000	0.000000	0.000000	0.000016	0.000000	0.000000	0.000000	0.000016	https://estatistica.madeira.gov.pt/
Black scabbard fish	0.000000	0.008244	0.000000	0.000000	0.000000	0.000000	0.000000	0.008244	https://www.ine.pt
Benthopelagic L	0.000000	0.000023	0.000000	0.000000	0.000000	0.000000	0.000000	0.000023	https://estatistica.madeira.gov.pt/
Benthopelagic M2	0.000000	0.000007	0.000000	0.000000	0.000000	0.000000	0.000000	0.000007	https://estatistica.madeira.gov.pt/
Epipelagic cephalopods S	0.000000	0.000000	0.000000	0.000000	0.000002	0.000000	0.000000	0.000002	https://estatistica.madeira.gov.pt/
Sum	0.002434	0.008531	0.006465	0.000163	0.000002	0.000152	0.000046	0.017793	

Table S4 – Average biomass contribution of each functional group as prey for other species (in %), and number of predators per each functional group in the Madeira system. Keystonenness index according to (Libralato et al. 2006). S – Small, M – Medium, L - Large

Prey	Nr. Predators	Prey (%)	Keystoneness index
Baleen whales	0	0.00	-0.19
Toothed whales	1	0.09	-1.21
Sperm whale	0	0.00	-0.07
Killer whales	0	0.00	0.09
Dolphins	2	0.28	0.18
Monk seal	0	0.00	-0.02
Shearwaters	0	0.00	-1.50
Small petrels	1	0.02	-2.00
Coastal birds	0	0.00	-0.004
Turtles	3	0.19	-1.03
Pelagic sharks	0	0.00	0.03
Deep-sea sharks	1	0.19	-0.61
Rays	1	0.14	-1.09
Bigeye tuna	1	0.19	-0.50
Skipjack tuna	2	0.28	-0.36
Other tunas	0	0.00	-1.45
Pelagic L	0	0.00	-0.26
Pelagic M	1	0.09	-1.01
Chub mackerel	11	3.06	-0.42
Blue Jack mackerel	13	2.78	-0.48
Pelagic S	17	4.80	-0.27
Epipelagic S/M	8	1.39	-0.66
Reef-associated L	1	0.09	-1.32
Reef-associated M	4	0.93	-0.66
Reef-associated S	10	1.76	-0.51
Benthopelagic M1	7	0.74	-0.76
Benthic S/M	8	1.25	-0.55
Demersal L	2	0.23	0.09
Demersal M	2	0.28	-0.07
Demersal S	6	0.65	-0.31
Black scabbard fish	1	0.09	-0.18
Benthopelagic L	2	0.19	-1.15
Benthopelagic M2	8	1.11	-0.30
Benthopelagic S	14	2.78	-0.49
Myctophids	26	6.20	-0.18
Mesopelagic S	16	3.33	-0.37
Bathydemersal L	1	0.19	-1.03
Bathydemersal M1	4	0.37	-0.55
Bathydemersal M2	7	0.83	-0.05

Bathypelagic M	9	1.30	-0.13
Bathydemersal S	8	0.93	-0.29
Epipelagic cephalopods S	14	2.13	-0.50
Mesopelagic cephalopods S/M	21	5.93	-0.27
Mesopelagic cephalopods L	5	1.85	-0.09
Crabs	13	3.56	-0.24
Shrimps	20	3.24	-0.004
Echinoderms	6	0.74	-0.36
Suprabenthic zooplankton	15	3.98	-0.33
Molluscs	13	2.50	-0.48
Other benthos	16	3.70	-0.34
Jellyfish	3	1.76	-0.23
Sessile filter feeders	3	0.28	-0.98
Zooplankton L	29	5.19	-0.48
Zooplankton S	29	14.49	-0.06
Macroalgae/seagrass	11	2.82	-0.25
Phytoplankton	8	2.22	-0.18
Detritus	18	8.89	

Figure S1 - The Mixed Trophic Impact (MTI) of the Madeira system. Blue and red squares represent the positive and negative impacts, respectively, between functional groups.

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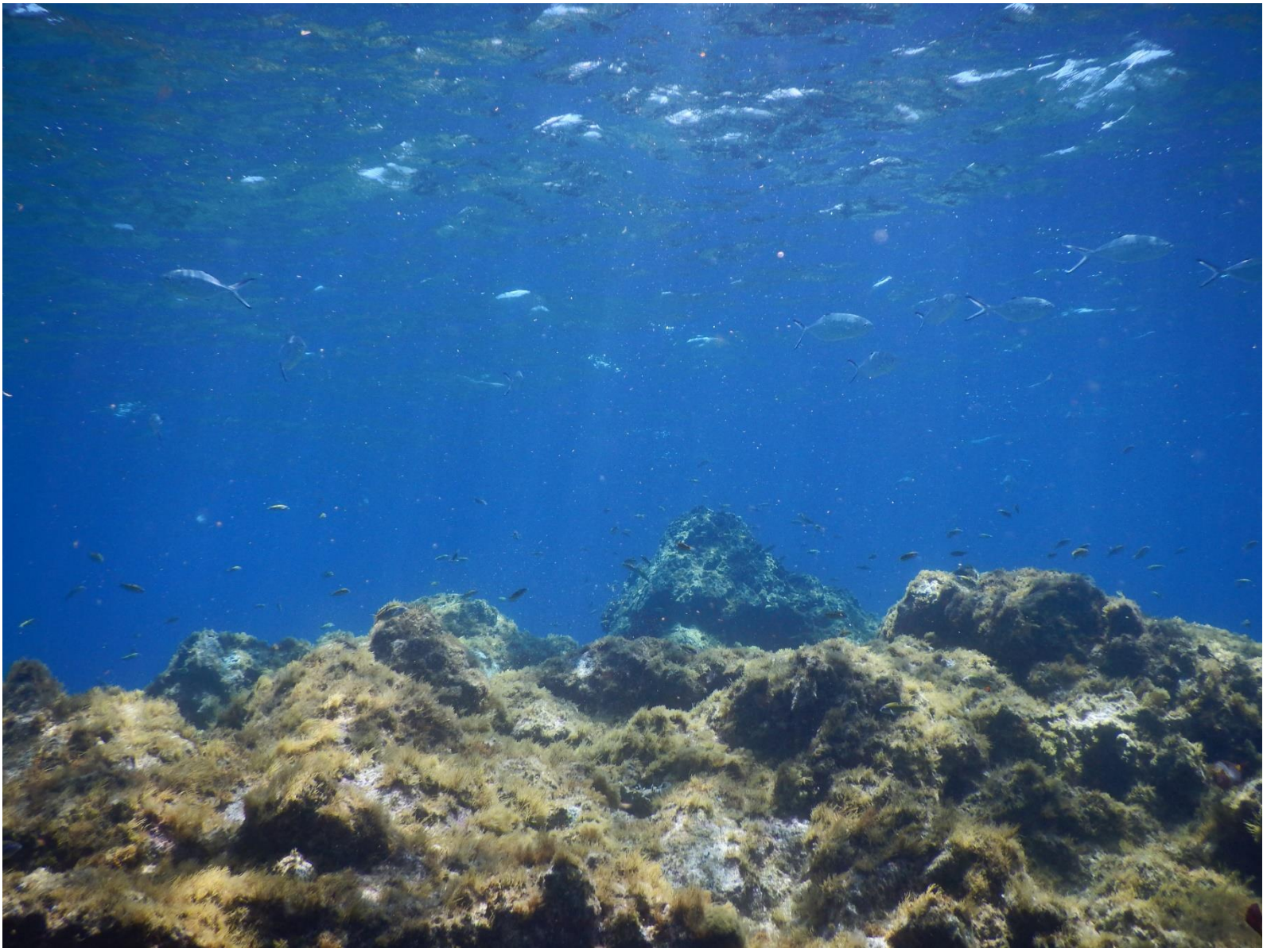
CHAPTER 7



Credits: Joana Romero

General Discussion

The studies in this thesis have contributed to the existing knowledge on oceanic regions by focusing on the diet and trophic interactions between some iconic species and groups found in the waters of the archipelago of Madeira. In Chapter 2, we described the diet of the two most abundant small pelagic species, the Atlantic chub mackerel *Scomber colias* and the Blue jack mackerel *Trachurus picturatus*, which also allowed us to have a first insight on the most common and abundant planktonic species in the region. In Chapters 3 and 4, we studied how top predators, namely tunas (3) and gulls (4), use the available marine resources around Madeira. In Chapter 5, we explored the interannual variability of the oceanic epipelagic fish and squid community through the study of the diet and foraging behaviour of the Cory's shearwater. Finally, in Chapter 6, we built a mass-balance model of the oceanic region of Madeira to study the structure and dynamics of its food web.

Diet, Prey abundance and Community assessment

Diet studies are important for the understanding of the ecology of species. Not only it reveals the prey composition, but also reflects the type of habitats used by the consumer and its foraging behaviour. The study of the diet of an organism also allows to explore interactions with other organisms or even with humans (Brodeur et al. 2008, Wallace et al. 2009), and to describe the prey community (e.g. Velarde et al. 1994) and its fluctuations (e.g. Velarde et al. 2015).

Despite the importance of tunas to the fisheries industry, our knowledge on their ecology is still very limited, especially in the Atlantic, where the feeding behaviour, vertical movements and migratory routes are some of the less studied topics. Tunas are difficult to observe or sample, and therefore more difficult to study, which is why collaborations with fishermen are important. Fishermen are key elements in the study of species targeted by fisheries, as *connoisseurs* of good sampling sites, and of how to find and capture those species more efficiently, which allows to achieve sufficient sample sizes. Still, some techniques used by fishermen might raise challenges in the study of the diet of tunas, or other species. In Madeira, and in a few other regions like the Azores and Canary Islands (Zeller et al. 2001), tunas are captured using live bait. The use of bait, together with showers, mimic the feeding frenzy phenomenon, which attracts tunas and facilitates their capture. However, during these events, tunas are likely to eat bait, which can bias the analysis of stomach contents. The analysis of the concentration of mercury

in the tissues of Bigeye and Skipjack tunas, and of two other predators, indicated that the Bigeye tuna did not have a mesopelagic diet, unlike in the north Pacific or equatorial Atlantic ocean (e.g. Ménard & Marchal 2003, Ohshimo et al. 2018). Instead, its diet was mostly composed by Atlantic chub mackerel and Blue jack mackerel (Chapter 3), depending to a large extent on epipelagic waters.

As mentioned before, diet studies are useful tools to assess prey communities. As such, top predators like seabirds and tunas, may constitute valuable sampling agents with associated low costs. They further provide near real-time information on the relative abundance and availability of commercial, non-commercial and unsurveyed species, extending sampling possibilities to less accessible organisms (Ainley et al. 1986). The conclusions on the diet of tunas (Chapter 3), allied to data collected on the diet and foraging areas of Cory's shearwaters (Chapter 5) and biomass estimations used to build the mass-balanced food web model (Chapter 6), allowed to conclude that among the intermediate trophic levels of Madeira, the most abundant groups in the pelagic ecosystem were myctophids, mackerels and flying squids. These were also the main groups sustaining other upper trophic levels and top predators, like marlins (e.g. Veiga et al. 2011), seabirds (e.g. Waap et al. 2017), and cetaceans (e.g. Fernández et al. 2009). Mesopelagic fish are among the most abundant fish families in these waters (Chapter 6), mainly represented by myctophids, like lantern fish of the genus *Diaphus* sp. and *Hygophum* sp. (Chapter 3). Blue jack and Atlantic chub mackerels are the most abundant epipelagic species in the region of Madeira (Chapter 3 and 5), together with Pilot fish (Chapter 5). The collection of regurgitations and GPS data of Cory's shearwaters over several years (Chapter 5), further revealed an increase in the population of Longspine snipefish *Macroramphosus scolopax* around the archipelago of Madeira in 2017/2018, suggesting a shift in the ecosystem of this oceanic region. Among cephalopods, the Neon and the European flying squids (Ommastrephidae) and Hooked squids (Onychoteuthidae), seem to be the most commonly distributed, according to the diet of tunas (Chapter 3) and Cory's shearwaters (Chapter 5).

The Atlantic chub mackerel and the Blue jack mackerel are the third most important sources of income for fishermen in Madeira, right after tunas and Black scabbardfish (*Aphanopus carbo* and *A. intermedius*; Hermida & Delgado 2016), and are also among the most important prey for top predators in the pelagic ecosystem. Describing their main prey is key to understand what sustains their populations. Both species revealed to be planktonic and piscivorous, feeding on dynoflagellates (*Lingulodium polyedra* and

Scrippsiella sp.), but also on diatoms of the family Bacillariophyceae and Pennales, and coccolithophores. They also fed on zooplanktonic species, like calanoid and cyclopoid copepods (*Candacia* sp., *Pleuromamma* sp., and *Oncea* sp.), and on very small Atlantic saury, clupeids, Longspine snipefish, myctophids and chub mackerels (Chapter 2). These results revealed the importance of long-term studies in marine environments. A previous study by Costa et al. (2013) briefly described the diet of Blue jack mackerel as being composed by fish and euphausiids. Although it is not possible to compare the fish species consumed, as Costa et al. (2013) did not identify them further, the planktonic species found in the mackerel's diet appear to be result of opportunism. In the face of shifts in the planktonic community, Blue jack mackerel seems capable to adapt its diet according to prey availability. The generalist and opportunistic behaviour of the Atlantic chub mackerel also suggests that shifts in its prey abundance and composition should not affect the population of Madeira significantly, which might indicate some resilience by these two species.

We also investigated the diet and foraging behaviour of the Yellow-legged gull in the archipelago of Madeira to understand how this top predator uses its marine environment (Chapter 4). Our study revealed that the Yellow-legged gull has an overall terrestrial behaviour with strong associations to anthropogenic sites and activities, like fisheries, but with low interaction with the marine environment. When at sea, around half of the trips were associated with purse-seine vessels. The low use of the marine environment by gulls in this region seems to be mostly related to the high availability of human refuse but also with a small fleet of purse-seiners and other near shore fisheries.

Food web structure and Fisheries

The oligotrophic oceanic region of the archipelago of Madeira has its overall biomass concentrated on the lower trophic levels, i.e. primary producers, zooplanktonic species, molluscs, suspension filter-feeders, and detritivores (Chapter 6), which are also the base of the food web and through which most of energy and matter flow. The food web was characterized by a more linear-like food chain in opposition to a more web-like food chain, with a big proportion of specialist organisms, like dolphins, shearwaters, and large pelagic fish. These species fed mainly on small pelagic and mesopelagic fish and cephalopods. Despite the low mean trophic level of the system, the mean trophic level of fisheries was 4.2, targeting mainly top predators, like tunas and Black scabbardfish, which

were also considered key components of the ecosystem, and with the most impact (Chapter 6).

In Madeira, top predators occur in large numbers and show high diversity. There, one can find a total of eight species of seabirds (Meirinho et al. 2014), 29 species of cetaceans (seven whales and 22 dolphins) (Freitas et al. 2012), five species of tunas (Gouveia et al. 2019), 27 species of sharks (both pelagic and deep-sea sharks; Biscoito et al. 2018), and many other predator fish, including the Blue and White marlins and the Black scabbardfish. According to our study in Chapter 6, top predators like sharks, dolphins and large demersal fish, were identified as important keystone species, meaning that they have a significant impact in the ecosystem, despite their low abundance, shaping the dynamics and functioning of food webs (Paine 1995). Our model suggested that the ecosystem should remain in equilibrium if fisheries are to continue exploiting the marine resources of Madeira at the same rate. Even so, it has been showed that the selective removal of certain species and size ranges will eventually deplete stocks and change the structure of the ecosystem (Zhou et al. 2010). For the scabbardfish, this can imply the disappearance of its population, as Madeira and the Canary Islands are its spawning grounds (Farias et al. 2013). For tunas, which are migratory species, it will ultimately depend mostly on the status of the population in the spawning and nursing areas. Since 1950, the total biomass of Bigeye tuna in the Atlantic has decreased 73%, of which 53% was in the last 30 years (ICCAT 2018). Although total landings have decreased since 1994, when catches reached a maximum of 134,933 tonnes, since 2006 catches have been slowly increasing again (ICCAT 2018). This is worrisome as ICCAT (International Commission for the Conservation of Atlantic Tunas) has defined this stock as overexploited. Similar decreasing and increasing trends of biomass and fisheries, respectively, have also been observed for Skipjack tunas in eastern Atlantic (ICCAT 2014). If the exploitation rate in the feeding areas remain unchanged, the populations of these three species will certainly continue to decrease and will have significant impacts on the structure of the food web, most probably impacting the epipelagic and deep-sea ecosystems, and consequently also impacting the economy of the archipelago of Madeira.

Fisheries do not only affect their targeted species, but can indirectly affect other species, like gulls. We have seen that gulls have a majorly terrestrial behaviour in Madeira. However, if for instance, the purse-seine fleet would increase in response to the depletion of stocks of higher trophic levels, or if regulatory measures would be applied to fisheries and/or to the main foraging area of gulls (landfills), Yellow-legged gulls could

be expected to increase their interaction with purse-seine vessels. There is a likelihood that gulls would also increase predation of small petrels. If these behaviour shifts were to be observed, gulls would consequently use more the marine environment and have a more substantial role in the marine food web of Madeira than presently.

Fisheries and climate change are known to cause alterations on life-traits of organisms, such as the reduction of their average length (Heino & Godø 2002, van Rijn et al. 2017), which can cause size-based trophic mismatches and perturbations on the prey-predator relationships. For instance, if the defence mechanism of a prey would be its size, then its reduction would increase the predation rate and, consequently, decrease its abundance. These are some of the consequences that can alter the types and strengths of flows of energy and matter in ecosystems, and impact the ecological networks and the ecosystem structure and functioning (Parmesan & Matthews 2006). Continued efforts to try to reduce pressure on fisheries and mitigate the consequences of climate change are needed to avoid irreversible changes in the structure of the ecosystem which cannot be compensated by its adaptation capacity.

Future research

This thesis has revealed new information on the diet and foraging behaviour of some iconic species from the archipelago of Madeira and has allowed us to have a better understanding of the trophic web of this ecosystem. But as expected, it also raises new questions to be answered. The study of the diet of the Bigeye tuna has revealed that in the archipelago of Madeira, this species is mainly feeding on epipelagic species, while it feeds on mesopelagic species elsewhere. Why would a species that tends to spend most of its time at higher depths, according to other studies (Brill et al. 2005, Junior et al. 2012), would feed on epipelagic species in the oceanic region of Madeira? This feeding behaviour should be further investigated focusing on the vertical movements of the tuna, but also on oceanographic phenomena which can affect their behaviour, and on the behaviour of their prey in Madeira. Long-term studies on the diet of Bigeye tuna are also important to better understand its feeding ecology.

In Chapter 5, we used the diet and foraging movements of the Cory's shearwater to show that very sudden and significant variations in this community can occur, as was the case of the appearance of the Longspine snipefish in the Selvagens region, which very quickly assumed a top position as prey for these seabirds in the region. Large scale and annual oceanographic variables did not explain the snipefish fluctuations. Further studies

on Longspine snipefish population dynamics and breeding biology in regions where its presence is more common, such as studies of oceanographic phenomena in the oceanic region of Madeira, may help shed more light on the drivers of these fluctuations. As done in chapter 5, it would be interesting to use other top predators, like the Bulwer's petrel or the Black scabbardfish, to describe the prey communities of deeper layers.

The Ecosim with Ecopath software, used to model the food web of Madeira, showed that there is still a lot to know about this ecosystem. Several species, mainly deep-sea species, have not been properly catalogued or sampled, which means that information on their biomass, diet, or reproduction biology are still unknown. Biomass was the most frequently missing parameter in the model, which shows the need for studies estimating population sizes.

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